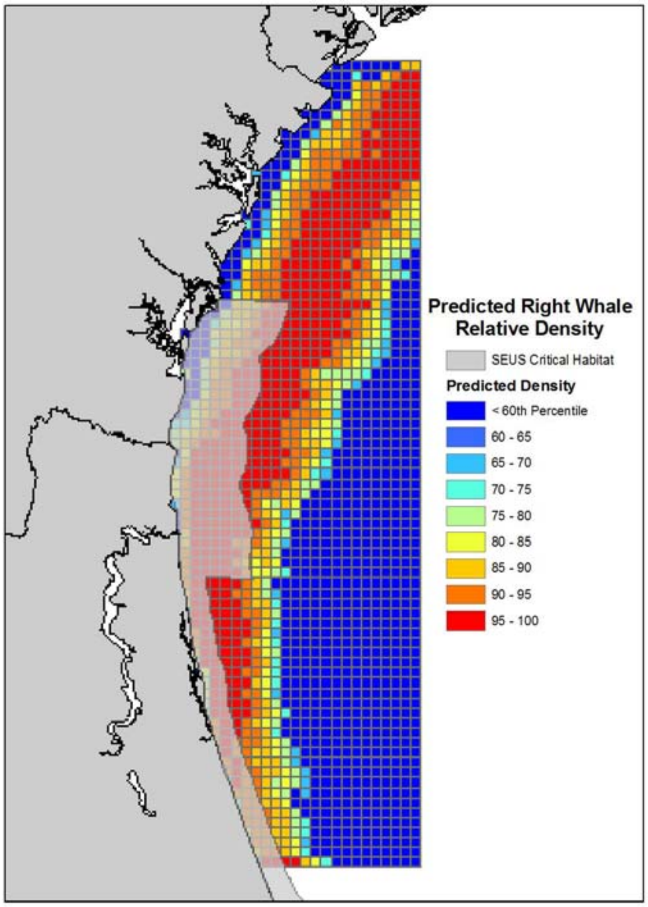
NOAA TECHNICAL MEMORANDUM NMFS-SEFSC-553

Defining the North Atlantic Right Whale Calving Habitat in the Southeastern United States: An Application of a Habitat Model



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March 2007

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NOTICE

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Executive Summary

A habitat analysis was conducted to examine the relationships between environmental characteristics and the spatial distribution of calving right whales in the southeast United States off of northern Florida and Georgia. A time series of right whale sightings data from aerial surveys conducted between December and March from 1992/1993 to 2000/2001 was used to assess habitat correlations and spatial patterns in right whale distribution. Satellite derived sea surface temperature, bathymetry, modeled average wind data, and several spatial variables were examined using a Generalized Additive Modeling approach. The model results indicate that sea surface temperature and water depth are significant predictors of calving right whale spatial distribution. The habitat relationships are unimodal, with peak sighting rates occurring at water temperatures from 13-15°C and water depths from 10-20m. These habitat features may be used to describe critical habitat areas off the coast of Florida and Georgia. The model also predicts that areas outside of the currently defined critical habitat are important for calving right whales. Recent surveys indicate that waters off of South Carolina and North Carolina are also frequently be used by calving right whales, and the habitat features identified in the current analysis are also present in these regions. However, additional data collection and analysis is needed before applying the predictions of the current model to these areas. The current analysis is developed as a tool for managers to define the spatial extent of right whale calving habitat and to designate revised critical habitat areas as defined by the Endangered Species Act.

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I. Background

Habitat is defined as the suite of environmental and biological characteristics necessary for the survival of an organism and persistence of a population (Harwood 2001). These environmental requirements (e.g., appropriate temperatures, salinities, food availability, etc.) are typically set by the physiology of the organism and the demands of life-history (e.g., socialization, breeding, and reproduction) that maintain the productivity of the population. . Under the Endangered Species Act (ESA), “critical habitat” is defined more specifically as: (i) the specific areas within the geographical area occupied by the species, at the time it is listed, in which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed that the National Marine Fisheries Service (NMFS) or the U.S. Fish and Wildlife Service determines are essential for the conservation of the species. Service regulations allow for designation of unoccupied areas upon a finding that occupied critical habitat is not sufficient for the conservation of the species (50 CFR 424.12(e)). Service regulations define physical or biological features essential to a species’ conservation as “primary constituent elements” (PCEs), that may include, but are not limited to, roost sites, nesting grounds, spawning sites, feeding sites, seasonal wetland or dry land, water quality or quantity, host species or plant pollinators, geological formations, vegetation types, tide, and specific soil types (50 CFR 424.12(b)). The ESA does not prohibit private individuals from affecting designated critical habitat, but requires each federal agency to insure, through consultation with NMFS, that its actions are not likely to destroy or adversely modify critical habitat.

For the North Atlantic Right Whale (*Eubalaena glacialis*), and other large whales, the two major habitat types are those that support feeding and calving (Harwood 2001). Recognizing these habitat requirements, NMFS designated critical habitat areas supporting feeding and calving areas in 1994 (50 CFR Part 226, Federal Register 59:28793). The summer feeding grounds in Cape Cod Bay, the Gulf of Maine and the Bay of Fundy have been intensively studied across multiple scales (e.g., Baumgartner et al., 2003; Baumgartner and Mate 2003; Kenney et al. 2001). The essential habitat feature, or PCE, of these feeding areas is high densities of copepods either near the water surface or at depths that are accessible to right whales (Kenney et al. 2001; Kenney et al. 1986). The spatial patterns and geographic areas of copepod densities sufficient for the feeding habitats in the Gulf of Maine have been reviewed and described by Pace and Merrick (2005).

While the habitat requirements for feeding are fairly well known, there has been comparatively little work characterizing the calving habitat for right whales. Extensive aerial survey data collected since the 1980's has shown persistent annual concentrations of calving female right whales in the southeastern United States in Northern Florida and Georgia (Kraus et al. 1986; Knowlton et al. 1994, Reeves et al. 2001). Calving right whales typically arrive in this region during late November and early December after migrating south from feeding grounds in the northeastern United States and Canada. Mothers and newborn calves reside within this region through early March, and they generally depart the calving grounds by the end of March and early April (Reeves et al. 2001). During the last decade, there has been strong interannual variation in the numbers of calving females arriving in the southeastern United States and therefore the number of calves they produced. The overall calving rate of the population may be correlated to food availability in the Gulf of Maine and Cape Cod Bay as related to large scale environmental factors including the North Atlantic Oscillation (Greene and Pershing 2004). There is no other known calving area for the North Atlantic right whale.

In addition, there is a component of the right whale population that does not summer in the Bay of Fundy/Gulf of Maine feeding grounds, and therefore are rarely sighted during summer surveys of these areas. These "non-Fundy" whales make up an unknown proportion of the right whale population. "Non-Fundy" mothers do, however, produce calves in the southeast calving grounds. Surveys in the calving habitats are one of the few times where these animals can be observed and photographed (Schaeff et al. 1993).

Recognizing the importance of the southeastern United States (SEUS) calving area to the conservation of the North Atlantic right whale, the region was designated as critical habitat under the ESA in 1994 (Federal Register 59:28793). The rule specifically considered habitat features that distinguished the near shore continental shelf off of Florida and Georgia as calving habitat. The rule noted that calving right whales may prefer habitat relatively close to shore (i.e., shallow water depths) due to the protection of the shoreline from wind and wave action that may disturb calves or increase the likelihood of separation from their mothers. The rule also discussed the thermal structure of the region, noting that the offshore portions of the area were dominated by high water temperatures (> 20 ºC) due to the presence of the Gulf Stream. Near shore waters were generally cooler, and right whale sightings were highest in water temperatures between 10-13 ºC (Federal Register 59:28793).

The geographic distribution of habitat features as correlated to right whale sightings resulted in establishment of a critical habitat boundary covering the near shore waters of the continental shelf between 31º 15' N and 30º 15'N extending 15 nautical miles from the shoreline. South of this area to 28º 00' N, the habitat designation narrows to within 5 nautical miles from the shoreline (Figure 1) reflecting both the narrowing of the continental shelf in this region and the approach of high temperature Gulf Stream waters fairly close to shore.

Since the designation of the critical habitat in 1994, there has been significant additional collection of aerial survey data and compilation of environmental data. In particular, the right whale "Early Warning System" aerial surveys have been conducted annually since 1992. These aircraft surveys are intended to provide information to mariners on right whale locations to allow alteration in course or vessel speed to reduce the risk of collisions. The surveys include primarily the critical habitat area, and they have more recently been extended both north and south of the critical habitat and further offshore. These data therefore provide significant additional information on the seasonal and interannual variability in the spatial distribution of right whales and associated habitat variables. In addition, since 2001, there have been several aerial surveys further north extending to North Carolina. During these surveys, there have been additional sightings of calving female right whales, including several animals that were not observed in the SEUS critical habitat area (W. McLellan, University of North Carolina at Wilmington, unpublished data; Wildlife Trust Incorporated, unpublished data). These additional data, along with compilations of environmental variables, are used here to examine the relationships between calving right whale spatial distribution and habitat characteristics and thereby develop a model for use in evaluating possible revisions to critical habitat boundaries.

II. Habitat Requirements for Calving Baleen Whales

A southern migration from cold-water feeding habitats for breeding and calving is a common feature among large whales. Baleen whales do not typically feed during the migration or residence period in the breeding/calving ground, and therefore migration imposes a significant energetic cost on males and females alike. The reasons for migration are likely a complex function of metabolic and social requirements. The most probable theories focus on improved probability of calf survival in the breeding/calving grounds relative to the feeding grounds. Three basic habitat requirements have been presented as factors that likely improve calf survival in lower latitudes. First, warmer water temperatures are likely to be necessary for calves that are born without the thick blubber layer of adults. Second, high latitude regions generally have higher average wind speeds, greater frequency of storms, and greater wave heights than the tropics during winter months. Calves are relatively weak swimmers and are likely to be easily separated from their mothers during storm events and in areas with high winds and waves. Separation from the mother for even a short time is likely fatal for newborn calves. Finally, it has been suggested that predation on calves may be reduced in tropical environments, though there is relatively little available data on the latitudinal distribution of predation rates on the calves of baleen whales (Corkeron and Conner 1999).

At smaller scales, within the calving and breeding habitats, there is additional evidence for spatial structuring of baleen whales dependent upon reproductive state. The prevailing theories for fine scale habitat partitioning focus on improvements in calf survival. In a breeding/calving ground for humpback whales in Madagascar, calving females and mother/calf pairs occurred closer to shore, in shallower habitats, and in areas more protected from wind and wave action than other members of the population (Erstes and Rosenbaum 2003). These locations are areas with calmer waters, and these habitat features may also be important because they offer protection from aggressive conspecifics. Breeding males are often aggressive and attempt to mate with females that already have a calf. This disturbance can injure a calf, separate it from the mother, and increase the energetic demands on both mother and calf. Areas closer to shore reduce the number of directions males may approach mother-calf pairs and provide a "back to the wall" form of protection. Shallower water likewise reduces the three-dimensional space available for approaches from larger males (Elwen and Best 2004a). Predators would likewise have a more limited range of approaches to attack calves and mothers. As with movements at larger scales, the fine scale habitat partitioning among conspecifics in calving habitats may be influenced by social and behavioral factors in addition to environmental constraints on mothers and calves (Erstes and Rosenbaum 2003; Elwen and Best 2004a).

Southern Right Whale Calving Habitat

The southern right whale, *Eubalaena australis*, also undertakes predictable seasonal migrations between high latitude boreal waters into temperate waters along the South African coast. The South African coast is oriented largely along an east-west axis across a spatial extent of approximately 800 km. The coastline is characterized by a series of coastal embayments and headlands that offer a range of protection from predominant wind and wave directions along with a range of substrates from hard rocky shorelines to sandy bottoms (Elwen and Best 2004a).

This region is a mating and calving ground, and mothers with calves typically have residence times of weeks to months (Best 2000). Based upon a long time series of aerial survey data and regional environmental data, Elwen and Best (2004a, 2004b) assessed the environmental features correlated with the spatial distribution of cow-calf pairs and unaccompanied whales. Mother-calf pairs occurred more frequently in bays that provided greater protection from prevailing wind and swell and over ocean floors with gentle slopes and sandy bottoms, and they were found generally closer to shore than unaccompanied whales (Elwen and Best 2004a,b).

Elwen and Best hypothesized that selection of protected, shallow water habitats by calving females is related to improved calf survival through both protection from conspecifics and clam wind conditions. However, they evaluated the reproductive effects of habitat variables and found that there was no difference in reproductive success based upon calving intervals as a function of spatial distribution and associated habitat variables (Elwen and Best 2004c). Spatial patterns in neonate strandings indicated that high calving mortality was correlated with the presence of non-cows, independent of environmental variables. These data suggest that social factors, including interactions with aggressive conspecifics, may outweigh environmental effects in determining the spatial distribution of calving females (Elwen and Best 2004c).

Features of the North Atlantic Right Whale Calving Habitat

There are important differences in both the social factors and physical features underlying the calving habitats of the North Atlantic right whale. Most notably, there is no evidence that the primary calving habitat is also the primary breeding ground. The vast majority of the sightings in the SEUS region are of either pregnant females or mother calf pairs. Immature whales and unaccompanied males and females are also seen during these surveys along with relatively large (6-10 whales) “surface active groups”. This may be a function of the relatively small population size, and it is certainly possible that breeding and calving occurred in the same places historically. At the current population size though, it does not appear that social factors and avoidance of aggressive conspecifics are as important for determining the spatial distribution of North Atlantic right whales as for other baleen whales.

The spatial structure of calving habitat features on the U.S. east coast is also quite different from that of the southern right whale along the South African coast. The coastline of the eastern U.S. is largely oriented in a north-south direction, and therefore there is a significant latitudinal gradient in water temperature not present on the South African coast. Winter sea surface temperatures range from less than 5 °C in New England and Gulf of Maine region to greater than 25 °C in waters off the coast of southern Florida. In addition, the presence of the Gulf Stream imparts a strong onshore-offshore gradient in water temperatures, particularly in areas south of Cape Hatteras, North Carolina. Gulf Stream waters typically have temperatures greater than 20 °C during winter, and water closer to shore is cooler ranging between 8-17 °C in the southern U.S. during winter months. In southern Florida, the warm Gulf Stream waters approach very close to the shoreline. In contrast to the situation in South Africa, the strong gradients in water temperature on the U.S. coast may have an important effect on the spatial distribution of calving right whales.

The bathymetry and shoreline shape of the southeastern U.S. is also quite different from that of the South African coast. The shoreline is smoother and does not have the same degree of complexity in the form of small protected embayments and rocky shorelines. The substrate type is uniform over the continental shelf south of the Gulf of Maine with a mixture of sand and mud, so the presence of rocky substrates that limited spatial distribution in South Africa is unlikely to be an issue. Finally, the slope of the bathymetry, particularly south of Cape Hatteras, is very shallow with water depths less than 50 meters extending up to 100 km from shore in South Carolina and Georgia.

III. Potential Calving Habitat Features

The prevailing theories describing the selection of calving grounds by baleen whales focus on improved survival for calves. The geographic areas that are optimal for calving will therefore contain a combination of environmental features that provide a significant increase in reproductive success over other areas.

Water Temperature Sea surface temperature (SST), as a proxy for water temperature throughout the water column, is expected to have an effect on the spatial distribution of calving right whales along the U.S. Atlantic coast. As homoeothermic animals, right whales expend additional energy for thermoregulation when temperatures are either too cold or too hot compared to some thermal optimum. Since right whales are cold adapted and have a thick layer of blubber, it is expected that they will be more sensitive to warm temperatures (e.g., Gulf Stream water) than colder temperatures. Newborn calves do not have the same thermal tolerance as adult whales, and it is therefore expected that calving females and mother-calf pairs have relatively narrow thermal tolerances. There are strong latitudinal and onshore-offshore gradients in temperature in the calving area, and these may limit calving right whale spatial distribution.

Water Depth Bathymetry has been cited as a feature of baleen whale calving habitats with calving females and mother-calf pairs preferring generally shallower waters than unaccompanied whales. Most of the presumed advantages of shallow water arise from reduced interactions with either predators or aggressive conspecifics because there is less opportunity for approaches to mother-calf pairs. It is unclear whether or not these factors will be important for the North Atlantic right whale where population sizes are low, and there is little information on predation on calves. Shallow water is also strongly correlated to other features associated with being relatively close to shore, including increased protection from wind and waves.

Wind and Wave Action Wind and wave intensity may be an important factor driving calving right whale spatial distribution on both regional and local scales. Along a latitudinal gradient, regions north of Cape Hatteras, North Carolina experience generally higher wind levels and greater frequency of winter storms than those south of North Carolina. Within a region, it is expected that wind intensities and wave heights will be generally lower close to shore where there is some sheltering effect of the shoreline. Calm waters have been cited as an important factor in calf survival for the southern right whale and other large whales due to the relatively weak swimming capabilities of calves.

Distance from Shore Areas relatively close to shore are characterized by shallow water depths, protection from wind and waves, and generally cooler water temperatures. Thus, this spatial variable may be an important consideration in calving right whale habitat since it is correlated with a number of important environmental features.

Bathymetric Slope For the southern right whale, areas with relatively gentle bathymetric slopes appeared to be a preferred habitat for mother-calf pairs. This is again likely to be correlated with other factors. Along the South African coastline, areas with relatively shallow bathymetric slopes also tended to be less exposed to wind and waves and with less exposure to deep, oceanic waters. On the southeastern U.S. continental shelf, the bathymetric slope is very shallow with water depths less than 50 m extending up to 100 km from shore off the coasts of Georgia and South Carolina. In southern Florida, the bathymetry is steeper with relatively deep waters approaching close to the shoreline. Due to the generally shallow bathymetry throughout the calving region, this factor is unlikely to be important for North Atlantic right whale calving habitat.

Bottom Sediment Composition Calving southern right whales also showed a preference for areas with sand and mud bottoms as opposed to rocky areas, again consistent with lower energy, shallow water, protected environments. The sediment composition throughout the southeastern United States is generally uniform with a sand-mud composition and relatively little exposed or rocky substrate aside from patches of hard bottom. Therefore, sediment composition is not an important factor for the North Atlantic right whale.

Social Factors Aside from environmental characteristics, several studies of baleen whales have shown that social factors are important in determining the spatial distribution of mother-calf pairs and driving fine scale partitioning of habitats. Because there does not appear to be extensive mating activity in the calving area and due to the low population size, it is unlikely that aggression from conspecifics is as important for the North Atlantic right whale as it may be for other baleen whales. However, there still may be a behavioral tendency for animals in similar life history stages to be closer together than may be expected from environmental features alone.

At larger scales, it is possible that the historically larger population used a larger range of habitats and geographic areas than is currently observed. Most large whales exhibit some degree of philotropy to particular calving, breeding, and feeding areas. It is possible that if a local population was extirpated during the whaling period, then this region would not be repopulated by the current right whale population. This effect is impossible to assess, but it may be a factor if regions that have suitable or even optimal calving habitat features are presently unoccupied.

IV. Methods – Modeling Right Whale Calving Habitat

The PCEs that define calving habitat for the North Atlantic Right Whale and the predicted geographic extent of the optimal calving area were assessed using a habitat modeling approach. Habitat modeling focuses on evaluating the "species-environment" relationships which model the occurrence of individuals as a function of various habitat characteristics (Austin 2002). These observed relationships with environmental features are then projected into geographic space to evaluate the physical extent and location of habitats. The general approach for habitat modeling is to evaluate the relationship between explanatory (i.e., environmental) variables and the occurrence of individuals or groups of individuals using regression methods.

Generalized Additive Models

Generalized additive models (GAM) are a flexible approach to exploring relationships between explanatory and response variables (Hastie and Tibshirani 1990). In contrast to the more familiar generalized linear models (e.g., linear regression), GAMs do not assume any particular functional relationship between the explanatory and response variables and instead use "smooth functions" to fit more complex curves whose shape is determined by the observed data. A number of smooth curve types can be fit to the observed data; however, for this application we have employed natural cubic splines because of the ability to specify the degrees of freedom and therefore the degree of smoothing of the data (Hastie and Tibshirani 1990). The basic form of the GAM model is:

$$(1) \qquad y = \theta_0 + \sum_i f(x_i)$$

where y is the response variable, $f(x_i)$ represents the smooth functions for each of i explanatory variables, and θ_0 is an intercept term. Due to its flexibility, the GAM approach has been applied to ecological problems including spatial patterns in fish trawl catches (Swartzman et al. 1992), factors effecting sighting probabilities for marine mammals during visual surveys (Forney 2000), and spatial models of cetacean abundance based on visual survey data (Hedley et al. 1999).

As with linear models, the GAM can take a range of functional forms (i.e., link function) and variance structures as appropriate for the expected statistical distribution of the data. In the case of counts of items within spatial cells, a Poisson distribution is appropriate as the response can take effectively any value from 0 to ∞. For these data types, a log-linear link function with Poisson error structure is an appropriate model for the number of events observed as a function of explanatory variables (McCullagh and Nelder 1989), and the form of the GAM function is:

$$(2) \qquad \log(N_k) = \log(E_k) + \theta_o + \sum_i f(x_{ik}),$$

where N_k is the expected count in a particular spatial cell k. The variable E_k is treated as an "offset" variable whose regression coefficient is equal to one, and it is appropriate where counts are standardized by some unit such as a time or area interval (McCullagh and Nelder 1989).

A Poisson error structure is assumed in this model, and therefore the expected value of the variance is equal to the mean. However, in most cases in spatial data there will be some degree of autocorrelation that results in deviation from this expectation, or "overdispersion", where the true variance is greater than that estimated by the Poisson model (McCullagh and Nelder 1989). Model fitting procedures in GAMs are generally accomplished by iteratively evaluating the deviance of the model, a quantity that is not sensitive to departures from assumptions about the variance structure. However, the calculation of standard errors around predicted values, and inferences about differences in predictions between two models, will be unreliable. Alternative non-parametric methods for variance estimation are therefore appropriate in the case of autocorrelated spatial data (e.g., Hedley et al. 1999).

Aerial Survey Data

The known calving ground is off the coast of northern Florida and Georgia where right whales have been observed to congregate annually between mid-November and the end of March. This region has been studied intensively by aerial survey during winter months (December – March) since 1992. The effort level has varied across the time series, but includes the latitude range from Savannah, GA (32.09 °N) to Ormond Beach, FL (29.34 °N). The most consistent survey effort has been expended in the "early warning system" (EWS) surveys from the shoreline to a distance approximately 18 nautical miles from shore. Additional coastal surveys included the Florida nearshore survey, beginning in January 1992, and the Georgia-nearshore surveys, beginning in January 1993. More recently, survey flights were added in the offshore region, east of the EWS, beginning in February 1996. The effort level has varied across the time series, but core survey areas were consistently flown.

LORAN-C or Global Positioning System (GPS) positions were sequentially recorded along the trackline to document flight and environmental conditions. When a whale was observed, the aircraft left the transect line to circle the whale for photo-documentation and to obtain a georeferenced position of the whale. An individual whale could have been repeatedly recorded on various surveys throughout the season.

The positions recorded during each flight were entered into a Geographic Information System (GIS) using customized programs to reconstruct and code each trackline. The digitally mapped trackline data were screened to use only the survey flight line flown under defined criteria (observers formally ‘on-watch’, sea states of Beaufort 3 or lower, altitude > 300 m, and visibility of at least 3.7 km). The resulting flight line was then buffered by 2.8 km on either side of the trackline to represent distance from the trackline that corresponds to the estimated search area (Hain et al. 1999). We used ARC/INFO’s GRID module to convert each georeferenced, vector map that depicted all of the area surveyed for a given day to a raster (cell-based) map, at 100-m resolution (100-m by 100-m cell size). To depict aerial effort for a given time period, raster maps representing searched areas within the time period were added together using map algebra. The resulting map for the time period shows the total effort per cell as the sum of all “flights” that covered that location (Figure 2).

Calving Right Whale Sightings

Between 1992-2002, a total of 1201 whale sightings were recorded in the study area. Only those sightings observed during surveys matching the standardized effort criteria were included in the analysis (n = 925). For this analysis, whale sightings were used rather than the number of observed individual whales per sighting since most sightings of multiple individuals were composed of a mother and her dependent calf.

Since this analysis was focused on calving habitats, the analysis was further restricted to include only mother-calf pairs or pregnant females. Pregnant females were individually identified using unique callosity patterns and the North Atlantic right whale photo-identification catalog maintained by the Right Whale consortium and curated by the New England Aquarium.

If a female is sighted with a calf during a given season, then it is known that the whale was pregnant during any previous sighting without a calf. Further, some individuals in the catalog are known to be males. Thus, using matches from photo-identification records, each sighting of an unaccompanied whale (i.e., not a cow-calf pair) was classified as either pregnant, male, or unknown. Photo-identification records were only available through the 2000/2001 season. A total of 545 sightings of cow-calf pairs or pregnant females (hereafter calving right whales) were used in this analysis along with survey effort data through the 2000/2001 season (Figure 3).

Habitat Variables

Sea Surface Temperature Advanced Very High Resolution Radiometer (AVHRR) imagery for the southeast U.S. was used to derive SST data. AVHRR data are acquired by sensors aboard NOAA Polar-Orbiting Operational Environmental Satellites and distributed by the National Environmental Satellite Data and Information Service (NESDIS). The southeast U.S. SST images extend from approximately 19º - 33º N latitude and 70º - 81º W longitude. The NOAA Coastal Services Center (CSC) provided imagery for the major portion of the study time period (spanning from December 1991 through February 1998, with the exception of December 1994 and January 1995). The remaining AVHRR images, including December 1994, January 1995, and December 1999 through March 2002 were obtained through the NOAA Coastwatch Program (http://coastwatch. noaa.gov/). All images sources were obtained for similar times of day (early afternoon).

The AVHRR data were collected from NOAA satellites nos. 7, 9, 11, and 14 – 16. AVHRR data for December 1991 – March 1993, February 1995 – March 1998, were atmospherically corrected using the NOAA/NESDIS multichannel SST algorithm to an accuracy of ± 0.7°C. The remaining Coastwatch imagery (December 1994-January 1995, December 1999-March 2002) was prepared by General Dynamics, Inc. Raw imagery values (digital numbers -

DN) were converted to degrees Centigrade using the formula: (DN-30)/6. All images have a spatial resolution (i.e., pixel size) of approximately 1.1 km. Images were georeferenced to an accuracy of ± 2 pixels.

Cloud and land pixels were excluded. A digital representation of the shoreline (1:100,000) was used to exclude imagery pixels that co-occurred with land. Pixels from the SST imagery from NOAA/Coastal Services with DN values > 245 (representing clouds) were also excluded. For the Coastwatch images, a total of seven cloud masks were provided along with each SST image. Each of the cloud masks was visually inspected, alone and in combination with others, to determine the best mask or combination of masks. A combination of three cloud masks removed cloud pixels to an acceptable degree without losing actual SST data in several test images, and so were used on all remaining AVHRR images. Not all cloud fringe was eliminated by the customary cloud masking algorithms, however. So additional pixels with values < 8ºC were eliminated based upon buoy data from the Gray's reef buoy, located in the northern portion of the study area. No temperatures below 8ºC had been recorded by the buoy in winter, and therefore pixels with lower temperature values were presumed to be contaminated by atmospheric humidity.

Bathymetry and Bathymetric Slope Bathymetry data for the continental shelf was obtained from digital elevation grids available from the National Geophysical Data Center (NGDC) Coastal Relief Model 3-arc second (~ 60m) resolution bathymetry grids for the U.S. continental shelf (http://www.ngdc.noaa.gov/mgg/coastal, Figure 1). Bathymetric slope was calculated as the difference between the minimum and maximum observed water depth within the 4x4 km spatial cells used to aggregate response and explanatory variables for this analysis (see below).

Average Wind Intensity There is no direct measure of wind intensities available at appropriate spatial resolution and extent for the current analysis. Therefore, wind intensity data were derived from a regional climate/weather model covering North America and the adjacent ocean waters developed by the National Center for Environmental Prediction (NCEP). The model spatial resolution is 32 x 32 km cells over a spatial extent ranging from approximately the Hawaiian islands on the western boundary to the central Atlantic ocean on the eastern side and from 1° north of the equator to 46 °N latitude.

The model (the North American Regional Reanalysis, NARR; http://wwwt.emc.ncep.noaa.gov/mmb/rreanl/index.html) is parameterized using weather observations from data stations on both land and water, and has been validated extending backwards in time to 1945. The model outputs include a large suite of weather variables resolved both horizontally and vertically at multiple levels into the atmosphere, and these are resolved temporally at 3 hour intervals. Model output on predicted winds (meters/second) at 10m above ground were used to calculate spatial grids of monthly average wind speeds during each season (1992/1993 – 2000/2001) for December – March (Figure 4).

Spatial Projection and Aggregation of Data

The boundaries of the study area encompassed the spatial extent of flight search area that included all survey types (NE corner 80º28’5”W, 32º8’29”N and SE corner 80º20’4”W,29º14’4”N, Figure 5). The study area comprised a total of 1,670 16-km^2 cells. All spatial data were projected into a custom Albers projection using the 1983 North American Datum. Data were then spatially aggregated into a 4 x 4 km cell size grid over the study area and temporally aggregated into semimonthly periods: from the 1st to the 15th day of the month, and from the 16th to the last day of each month. Effort data was summed across each period, resulting in a 100 m resolution raster image depicting the number of times a cell was searched over each approximately two-week period. All available AVHRR images with coverage of greater than 10% of the study area were used to develop an average SST for each period at a 1.1-km cell size resolution. Cells with no data were ignored in the temporal aggregations.

SST, bathymetry, search effort, and average monthly wind intensity were averaged within each 16-km^2 cell for each biweekly period. Bathymetric slope was derived within each spatial cell as described above. The total number of calving right whale sightings (i.e., groups of animals) was summed within each cell (e.g., Figure 5) for each biweekly period.

Spatial information including the relative north-south location (i.e., “Northing”), east-west location (i.e., “Easting”), and distance from shore were calculated based upon the mid-point of each cell location. Distance from shore was calculated as the closest distance between a high-resolution coverage of the coastline and the mid-point of the spatial cell.

Model Selection and Fitting

A log-linear generalized additive model (GAM) with a Poisson error structure was used to evaluate the relationship between calving right whale sightings (i.e., a group of animals observed at a particular spatial location) and environmental variables. Each 4x4 km cell was considered a sampling unit in this analysis. The total number of flights in the cell for a particular time period was included in the model as an “offset” variable to account for the effects of survey effort. Natural smoothing splines were used as the smoothing function in the GAM fits (Venables and Ripley 1997). Preliminary analyses indicated that second order functions (i.e., natural smoothing splines with 2 degrees of freedom) were the most appropriate for all environmental variables.

There has been strong interannual variability in the numbers of calving right whales in the SEUS calving ground during the last decade. This variability is the result of processes occurring outside of the seasonal and spatial time frame of the surveys in the calving area such as overall population health and food availability in the northern habitats. The interannual effects must be included in fitting the model to observed data; however, no attempt is made to infer the underlying relationships with environmental variability or to develop a predictive model of annual variation in absolute numbers. These effects were accounted for in this analysis by including survey year as a factor variable with 9 levels.

Selection of significant environmental variables was accomplished through a forward selection approach. Beginning with the “offset-only” model including no effects other than the offset term, each environmental variable was added individually. The importance of the variable was assessed using Akaike’s Information Criterion (AIC) which balances the explanatory power of the variable against the increase in model degrees of freedom by including the term to develop the most parsimonious model. In comparing two models, a reduction in the AIC value indicates an improvement in explanatory power. For all factors resulting in a significant reduction in AIC over the “offset-only” model, higher order (i.e., two and three term) models were tested, in each case evaluating the importance of adding additional variables by the reduction in AIC.

Bootstrap Resampling Approach To Model Fitting

The division of the sampling area into 1670 spatial cells, 8 biweekly time intervals, sampled over 9 seasons results in 120,240 “sampling units”. However, these cells cannot be considered independent degrees of freedom in the GAM analysis. First, the number of cells (and therefore model degrees of freedom) is dependent upon the cell size at which the analysis is resolved. Second, cells were actually sampled along temporally varying transect lines, and there is thus spatial and temporal dependence between cells in the sampling design. Finally, there is spatial autocorrelation in both environmental factors and the distribution of right whales that reduces the independence between sampled cells.

A bootstrap resampling approach was used to reduce the spatial and temporal dependence between cells. For each bootstrap iteration, 1670 cells were randomly sampled, with replacement, for each of the 8 biweekly periods in the survey. The cells with survey effort were used as the sampling units in the GAM analysis for that iteration. Thus, each bootstrap sample reflects the sampling intensity for a "typical" survey year in each biweekly interval (typically ~5700 cells). The GAM analysis, including forward selection of model terms, was conducted for each of 500 bootstrap iterations and model fit, output, and predicted values were stored. Summaries of model fits and predictive capability were based upon median values from the bootstrap iterations, and model uncertainty was calculated from the observed variance in the bootstrap distribution.

V. Habitat Model Results

The stepwise model selection indicated that the annual effects, sea surface temperature, and water depth were the significant predictor variables for the spatial distribution of calving right whales. The annual terms followed by depth resulted in the greatest reduction in the median AIC (Table 1). The addition of sea surface temperature resulted in a further median reduction in AIC. However, SST was also strongly correlated with the spatial variables (East and North), and thus similar reductions were achieved when adding these variables into the model. Once SST was added to the model, no additional model terms, including the spatial terms, resulted in significant reductions in AIC. The selected model was highly significant (Median chi-square = 94.32, df = 28, p << 0.0001) and explained 21.3% of the total variation in right whale spatial distribution (Approximate R-square after Nagelkerke, 1991).

The inclusion of annual terms as a factor effect resulted in exactly fitting the average SPUE and predicted right whale sightings for each season (Figure 6). This is the intended result of this approach since the factors driving the total abundance of calving right whales in the SEUS occur independently of the environmental and spatial variables measured in the current study.

The model including temperature and depth effectively modeled the sighting rates as a function of environmental variables (Figure 7). The highest observed and predicted sighting rates occurred at water temperatures between 13-15 °C. Peak sighting rates occurred in water depths between 15-25 m, and sighting rates declined dramatically at water temperatures greater than 17°C (Figure 7, Figure 8).

Cross-validation of model predictions was performed by regressing the observed vs. predicted number of right whale sightings in 1°C temperature and 1-m depth intervals for two sample years (Figure 9). A perfect model prediction in these figures would have a slope and r-square value equal to 1. The model is more effective at predicting sightings in the year with the higher abundance of whales. The model also tends to predict higher than observed sightings in each environmental cell during the 2000/2001 season. This is a typical feature of habitat models as the available habitat area is typically larger than that occupied by the organisms, particularly for a relatively low abundance animal like right whales.

The habitat model was effective at predicting the observed spatial patterns in right whale sightings when accounting for the distribution of survey effort and environmental variability. During the 1996/1997 season, the number of right whales observed was generally low (Figure 6). The relatively few sightings in December occurred near the middle of the survey area, though sighting rates were predicted to be higher in the northern portion of the area (Figure 10a). During January, right whale sightings occurred in the northern portion of the habitat, and in the southern portion of the habitat in February. These observations are consistent with the spatial pattern predicted by the habitat model (Figure 10b-d).

In the 2000/2001 season, right whale sightings were more evenly distributed through the habitat area during December and January, were concentrated in the southern and central portion of the habitat during February, and were in the southern part of the habitat during March. The spatial patterns in sightings were similar to those predicted by the habitat model (Figure 11a-d).

The time averaged predicted SPUE of calving right whales in the SEUS region are shown in Figures 12-15. These surfaces reflect the average water temperatures in each spatial cell across the time series and are averaged across annual effects. This surface is a proxy for the predicted relative density of right whales across the area for each biweekly interval independent of levels of survey effort. Several large scale spatial patterns are apparent from these plots. First, the region offshore of Georgia that has relatively low survey effort in offshore waters is an area with consistently high predicted sighting rates through much of the right whale season. As the season progresses from December to February, the highest peak sighting rates extend further south into the habitat, associated with the seasonal latitudinal progression of favorable water temperatures. In the southern portion of the area, the predicted peak sighting rates are confined to areas relatively close to shore associated with both increasing water depth in this area and the associated incursion of warm waters influenced by the Gulf stream close to shore.

In summary, water temperature and depth are significant predictors of right whale spatial distribution in the SEUS calving region. The observed spatial distribution of calving right whales, after accounting for the distribution of survey effort, is strongly correlated with interannual and within-season variations in the distribution of water temperature. During colder years, and during colder months of the calving season, right whale spatial distribution tends to shift both further south and further offshore relative to warmer periods. Peak predicted and observed calving right whale sighting rates occur within the relatively narrow environmental ranges of 10-20m water depth and 13-15°C. The model results indicate that these environmental ranges describe the habitat requirements for calving right whales.

VI. Defining Right Whale Calving Habitat Boundaries

Describing fixed geographic areas that are expected to contain the calving habitat is a significant challenge for defining critical habitat for management purposes. First, in marine environments, there is strong temporal variability in the spatial distribution of important habitat variables. In the current analysis, sea surface temperature is the critical spatial variable, and its spatial distribution fluctuates on seasonal and annual time scales. Second, the distinction between "habitat" and "not habitat" implies a clear boundary or binary characteristic of the environment. In terrestrial environments, landscape features can often be defined by some clear and fixed boundary, for example the edges of a stream bed or flood plain. However, in the current case habitat is best represented as a spatial gradient between the most suitable and least suitable environments. There is no clear spatial boundary for the habitat, and no boundary to the movement of right whales inside and outside of the optimal habitat.

The definition of a geographic area that encompasses the “critical” habitat is a decision to be made by management. In an effort to avoid any potential impacts on habitat, and therefore calving right whales, one could potentially define a geographic area that contains even marginal habitat characteristics. This region would be relatively large and contain a significant amount of space where right whales only occasionally occur either because the environmental characteristics are marginal or because the most suitable habitat only rarely occurs in the area.

In contrast, one could make a more restrictive definition such that only the geographic region that consistently contains the “best” habitat would be included in the management area. This would be a smaller geographic region, reducing the impact and extent of potential management actions, and would exclude some areas that may frequently contain both suitable habitat and right whales.

The habitat model developed here is used to describe the potential limits of a geographic boundary for the calving ground based upon a long-term average of predicted sighting rates. Decisions on habitat boundaries for management purposes can be made based upon the relative average suitability of habitat within spatial cells.

Relative Average Habitat Suitability

For each spatial cell, the average water temperature was calculated across the time series. The predicted average SPUE based upon the mean temperature and depth within the cell was developed from the habitat model. These average SPUEs were then ranked into percentiles. Thus, the spatial cells with the most suitable average environmental conditions were in the highest percentiles. The surface of percentiles for 1°C SST and 1-m water depth intervals is shown in Figure 16. The peak habitat ranges (13-15°C and 10-20m depth) correspond to predicted sighting rates in the 95th-99th percentile.

Spatial cells in the highest percentiles of predicted SPUE contain the great majority of right whale sightings during these surveys (Table 2, Figure 17). Cells with in the top 5% of predicted SPUE (>95th percentile) account for 43.5% of all observed calving right whales, and those in the top 10% (> 90th percentile) include 66% of all sightings (Table 2). This reflects the relatively concentrated spatial distribution of peak right whale densities rather than simply the spatial distribution of survey effort. While the majority of survey effort is concentrated in the most suitable habitat areas, the cumulative distribution of sightings deviates from that of the survey effort (Figure 17) demonstrating that sighting rates peak sharply in the spatial cells encompassing the most suitable environmental characteristics.

Projecting these average environmental patterns into geographic space provides the basis for defining fixed calving habitat boundaries. The percentile of predicted SPUE along with average observed SST in each spatial cell are shown in Figure 18. Outlining the contours in percentiles of SPUE result in spatial habitat boundaries (Figure 19). For example, defining habitat as all spatial cells in the highest 5% of predicted SPUE encompasses spatial cells containing 44% of all historical calving right whale sightings. The resulting area extends further north than the currently defined critical habitat and further offshore of the coast of Georgia. However, this boundary does not include areas further south and offshore of Florida (Figure 19). Defining calving habitat based upon the 75th percentile would include areas further offshore of Florida and further south. This larger region would include 91% of all historical sightings (Table 2, Figure 19).

Conclusions and Habitat Definitions

The results of this analysis indicate that areas further north and further offshore than the currently defined critical habitat boundary include suitable average environmental conditions and resulting high sighting rates of calving right whales. Decisions about critical habitat boundaries for management can be made on the basis of the relative average suitability of habitat within spatial cells. The approach described here provides a mechanism to define spatial cells as habitat based upon their average environmental conditions and the resulting use of these areas by calving right whales.

VII. Potential Right Whale Calving Habitat Further North

The currently defined right whale calving critical habitat was initially based upon a relatively limited number of survey flights during the late 1980s and early 1990s. The region off of northern Florida and Georgia was an area with the most consistent sightings of right whales, and the area was identified as the only known calving ground for right whales. In addition, management requirements associated with shipping and military activities at the three major southeastern ports (Jacksonville, FL, Fernandina, FL, and Georgia, FL) have resulted in the development and maintenance of the Early Warning System flights that make up the basis of the current analysis.

Until recently, there has been very little systematic effort to evaluate calving right whale spatial distribution outside of this region. There are numerous sightings along the mid-Atlantic coast between Georgia and North Carolina in non-systematic and opportunistic surveys, including sightings during winter months (Knowlton et al, unpublished results). More recently, systematic aerial surveys off the coast of North Carolina have been conducted during December – February of 2002. These surveys observed several mother-calf pairs during winter months, some of which were never observed in the calving area off of Florida and Georgia (W. McLellan, University of North Carolina at Wilmington, unpublished results). Systematic surveys were also conducted during the winter of 2005 off the coast of South Carolina, and these surveys also observed calving right whales throughout the winter. Finally, passive acoustic monitoring for right whale calls was conducted during the winter of 2004, and right whale contact calls were detected during February and March at buoys near Cape Lookout, NC and off of Charleston, SC (C. Clark, Cornell University, pers. comm.). Each of these survey activities is ongoing, and they continue to document the use of the region from Georgia to North Carolina by calving right whales during winter months. However, it is unlikely that whales occur in these areas at the density and consistency of the use in the Florida/Georgia region.

Given this documented use of the region between South Carolina and North Carolina by calving right whales, it is appropriate to evaluate the spatial extent of the habitat characteristics identified in the current analysis. The bathymetry off the coast of South Carolina and southern North Carolina is generally shallow, with water depths less than 30 m extending up to 80 km offshore (Figure 20). Winter water temperatures on the continental shelf generally range between 12-18°C throughout this region, with generally cooler waters very close to shore and high temperature waters generally occurring well offshore beyond the shelf break (Figure 21). There is the expected seasonal progression of temperatures such that the optimal temperature range, and peak predicted sighting rates, for calving right whales occurs throughout much of the spatial range in waters typically between 10 to 50 km from shore (Figure 22). Based upon the mean water temperatures between December-March, the model developed here predicts appropriate calving habitat for right whales over much of the continental shelf south of Cape Fear, North Carolina (Figure 23).

There are some potentially significant caveats to the extension of critical habitat further north based upon the current analysis. First, the current data and model only reflect the spatial processes observed in the Florida-Georgia region. Environmental/spatial relationships may not follow the same patterns outside of this region. For example, the slope of bathymetry off of South Carolina is different from that off of Florida, and shallow water depths occur further from shore. As noted in the discussion above, water depth may be a proxy for distance from shore, and thus the strong relationship with depth observed off of Florida may be expected to break down off of South Carolina. In addition, there is a strong regional pattern in wind speeds, with generally higher average winds off shore of South Carolina and North Carolina during winter months. Wind speed was not important in the model developed for the region offshore of Florida and Georgia; however, there is also relatively little spatial variation in average winds within this area. The relationships observed off of Florida and Georgia may not reflect processes offshore of South Carolina and North Carolina, and therefore considerable caution should be used before extending the predictions of the model further north.

In addition to these data and extrapolation issues, the areas of North Carolina and South Carolina may be appropriate habitat, yet may still not be used as a calving ground due to social or historical factors. In general, the spatial range used by a species contracts when abundances are low, as is the case for right whales. Thus, even appropriate habitats may not be used even though they could be important if population size becomes larger. In addition, large whale populations frequently show philotropy to particular areas. If, for example, a sub-section of the current population historically occupied calving grounds off of South Carolina, and this subpopulation was extirpated, then these areas are unlikely to be recolonized by other segments of the population even though they represent suitable habitat. The "non-Fundy" whales may well reflect a remnant subpopulation, and some of these animals have been observed in mid-Atlantic habitats.

North of Cape Hatteras, North Carolina along the U.S. east coast to New York, there is a dramatically different spatial relationship between habitat characteristics. During winter months in this region, water temperatures over the continental shelf are generally less than 10 °C and water in the optimal range of 13-15 °C occurs only well offshore over the inner continental slope. The nearshore bathymetry is also much steeper with water depths in the range of 10-20 m extending only 10-15 km from shore. Average wind speeds are also consistently higher than those along the southeast coast and range between 10-14 knots compared to 4-6 knots. Therefore, based on the model results and data used here, there is no expectation that suitable winter calving habitats occur north of North Carolina.

Water temperatures and depths that are consistent with optimal habitat for calving right whales occur over the continental shelf from northern Florida to Cape Fear, North Carolina. However, the current analysis does not provide sufficient information to assume that the habitat relationships observed in the currently defined calving grounds are maintained further north. Ongoing analyses of data presently being collected will be useful in evaluating the predictions of the current model for these regions.

VIII. Conclusions

Critical habitat areas are designated by evaluating the spatial distribution of habitat features that are essential to the demographic processes that maintain the survival of an endangered species or management unit. In the current analysis, a habitat model was developed for calving right whales in the region off the coast of northern Florida and Georgia. The model is an effective predictor of the spatial distribution of calving right whales and tracks seasonal and interannual variability in spatial distribution in response to the changing spatial pattern of habitat features. The data indicate that water temperatures between 13-15°C and water depths between 10-20m are optimal habitats for calving right whales. The average spatial patterns in these habitat features can be used to define fixed boundaries for critical habitat. Based on these results, it appears that the currently defined critical habitat should be expanded to include areas further offshore and generally further north off the coast of Georgia. Optimal water temperatures and depths also occur off the coasts of South Carolina and North Carolina, however the available data are currently insufficient to evaluate whether or not these regions are also optimal calving habitats. More systematic data collection in these areas, and additional analyses, will allow additional assessments of potential calving habitats, and the use of those habitats, along the southeast U.S. coast.

Literature Cited

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modelling* 157:101-118.

Baumgartner, M. F., T. V. N. Cole, P. J. Clapham and B. R. Mate. 2003. North Atlantic right whale habitat in the lower Bay of Fundy and on the SW Scotian Shelf during 1999-2001. *Marine Ecology Progress Series* 264:137-154.

Baumgartner, M.F. and B.R. Mate. 2003. Summertime foraging ecology of North Atlantic right whales. *Marine Ecology Progress Series* 264: 123-135.

Best, P. B. 2000. Coastal distribution, movements, and site fidelity of right whales, *Eubalaena australis* off South Africa, 1969-1998. *South African Journal of Marine Science* 22:43-55.

Corkeron, P.J. and R.C. Connor. 1999. Why do baleen whales migrate ? *Marine Mammal Science* 15(4): 1228-1245.

Elwen, S.H., and P.B. Best. 2004a. Environmental factors influencing the distribution of southern Right Whales (*Eubalaena australis*) on the South coast of South Africa I: Broad scale patterns. *Marine Mammal Science* 20(3): 567-582.

Elwen, S.H., and P.B. Best. 2004b. Environmental factors influencing the distribution of southern Right Whales (*Eubalaena australis*) on the South coast of South Africa II: Within bay distribution. *Marine Mammal Science* 20(3): 583-601.

Elwen, S.H. and P.B. Best. 2004c. Female southern right whales *Eubalaena australis*: Are there reproductive benefits associated with their coastal distribution off South Africa ? *Marine Ecology Progress Series*. 269: 289-295.

Erstes, P.J. and H.C. Rosenbaum. 2003. Habitat preference reflects social organization of humpback whales (*Megaptera novaengliae*) on a wintering ground. *Journal of Zoology*. 260: 337-345.

Forney, K. 2000. Environmental models of cetacean abundance: reducing uncertainty in abundance trends. *Conservation Biology*. 14: 1271-1286.

Greene, C.H. and A.J. Pershing. 2004. Climate and the conservation biology of North Atlantic right whales: the right whale at the wrong time ? *Frontiers in Ecology and the Environment* 2(1): 29-34.

Hain, J.H.W., Ellis, S.L., Kenney, R.D., and C.K. Slay. 1999. Sightability of right whales in coastal waters of the southeastern United States with implications for the aerial monitoring program. *In:* Garner, G.W., Amstrup, S.C., Laake, J.L., Manly, B.F.J., McDonald, L.L., and D.G. Robertson (eds). Marine Mammal Survey and Assessment Methods. AA Balekma, Rotterdam, pgs. 179-190.

Hastie, T.J., and R.J. Tibshirani . 1990. Generalized additive models. Monographs on Statistics and Applied Probability 43. Chapman and Hall, London 335 pp.

Harwood, J. 2001. Marine mammals and their environment in the twenty-first century. *Journal of Mammology* 82(3): 630-640.

Hedley, S.L., Buckland, S.T., and D.L. Borchers. 1999. Spatial modeling from line transect data. *Journal of Cetacean Research and Management*. 1: 255-264.

Kenney, R. D., M. A. M. Hyman, R. E. Owen, G. P. Scott and H. E. Winn. 1986. Estimation of prey densities required by western North Atlantic right whales. *Marine Mammal Science* 2:1-13.

Kenney, R. D., C. A. Mayo and H. E. Winn. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales. *Journal of Cetacean Research and Management* Special Issue 2:251-260.

Kraus, S. D., K. E. Moore, C. E. Price, M. J. Crone, W. A. Watkins, H. E. Winn and J. H. Prescott. 1986. The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). Pages 145-151 *in* R. L. Brownell, Jr., P. B. Best and J. H. Prescott, eds. *Right Whales: Past and Present Status*. International Whaling Commission, Cambridge, U.K.

Knowlton, A. R., S. D. Kraus and R. D. Kenney. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Canadian Journal of Zoology* 72:1297-1305.

McCullagh, P. and J.A. Nelder. 1983. Generalized linear models. Chapman and Hall, New York, New York.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78:691-692.

Pace, R.M. and R.L. Merrick. 2005. Potential Primary Constituent Elements for Right Whales (*Eubalaena glacialis*) in the Northwest Atlantic Ocean. NMFS, Northeast Fisheries Science Center. Woods Hole, MA 02543.

Reeves, R. R. 2001. Overview of catch history, historic abundance and distribution of right whales in the western North Atlantic and in Cintra Bay, West Africa. *Journal of Cetacean Research and Management* Special Issue 2:187-192.

Schaeff, C. M., S. D. Kraus, M. W. Brown and B. N. White. 1993. Assessment of the population structure of western North Atlantic right whales (*Eubalaena glacialis*) based on sighting and mtDNA data. *Canadian Journal of Zoology* 71:339-345.

Swartzman G., Huang C., and S. Kaluzny. 1992. Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1366-1378.

Venables W.N. and B.D. Ripley. 1997. Modern applied statistics with S-PLUS. Springer-Verlag, NY, 548 pp.

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Table 1. Sequential addition of terms to the "offset only" model and the reduction in median AIC for each term. The best model included terms for effort, survey year, water depth, and sea surface temperature.

#	Model Terms	Degrees of Freedom	Median AIC	Contrast	Delta AIC
1	log(Effort) - offset only	1	474.1		
2	log(Effort) + Annual Terms	9	425.2	2 vs. 1	48.9
3	log(Effort) + ns(East, 2)	3	466.7	3 vs. 1	7.4
4	log(Effort) + ns(North, 2)	3	468.4	4 vs. 1	5.7
5	log(Effort) + ns(Distance From Shore, 2)	3	463.1	5 vs. 1	11.0
6	log(Effort) + ns(SST, 2)	3	450.3	6 vs. 1	23.8
7	log(Effort) + ns(Depth, 2)	3	460.0	7 vs. 1	14.1
8	log(Effort) + ns(Depth Gradient, 2)	3	475.3	8 vs. 1	-1.2
9	log(Effort) + ns(Wind, 2)	3	470.3	9 vs. 1	3.8
10	log(Effort) + Annual Terms + ns(SST,2)	11	413.1	10 vs. 2	12.1
11	log(Effort) + Annual Terms + ns(Depth,2)	11	412.2	11 vs. 2	13.0
12	log(Effort) + Annual Terms + ns(DFS,2)	11	414.3	12 vs. 2	10.9
13	log(Effort) + Annual Terms + ns(East,2)	11	414.0	13 vs. 2	11.2
14	log(Effort) + Annual Terms + ns(North,2)	11	418.0	14 vs. 2	7.2
15	**log(Effort) + Annual Terms + ns(Depth,2) + ns(SST,2)**	**13**	**405.4**	15 vs. 11	**6.8**
16	log(Effort) + Annual Terms + ns(Depth,2) + ns(East,2)	13	405.4	16 vs. 11	6.8
17	log(Effort) + Annual Terms + ns(Depth,2) + ns(North,2)	13	406.0	17 vs. 11	6.2
18	log(Effort) + Annual Terms + ns(Depth,2) + ns(DFS,2)	13	409.7	18 vs. 11	2.5

Table 2. Distribution of right whale sightings and survey effort as a function of the percentile of predicted SPUE from habitat model.

Percentile of SPUE	Right Whale Sightings	Cumulative Proportion of Sightings	Total Effort (Flights)	Cumulative Proportion of Effort
< 5th	0	0.000	917	0.005
5th - <10th	0	0.000	617	0.008
10th - <15th	0	0.000	1,013	0.013
15th - <20th	0	0.000	1,813	0.022
20th - <25th	1	0.002	1,797	0.031
25th - <30th	0	0.002	1,678	0.039
30th - <35th	1	0.004	1,212	0.045
35th - <40th	0	0.004	2,590	0.058
40th - <45th	0	0.004	1,554	0.066
45th - <50th	1	0.006	1,518	0.074
50th - <55th	2	0.009	3,183	0.090
55th - <60th	3	0.015	7,328	0.126
60th - <65th	3	0.020	6,070	0.157
65th - <70th	9	0.037	9,696	0.205
70th - <75th	15	0.064	6,484	0.238
75th - <80th	16	0.094	6,802	0.272
80th - <85th	40	0.167	20,747	0.376
85th - <90th	93	0.338	21,897	0.485
90th - <95th	124	0.565	32,737	0.649
95th - 99th	237	1.000	70,125	1.000

Figure 1. The right whale calving area off the coast of Florida and Georgia showing the critical habitat boundary (cross-hatch) designated in 1994.

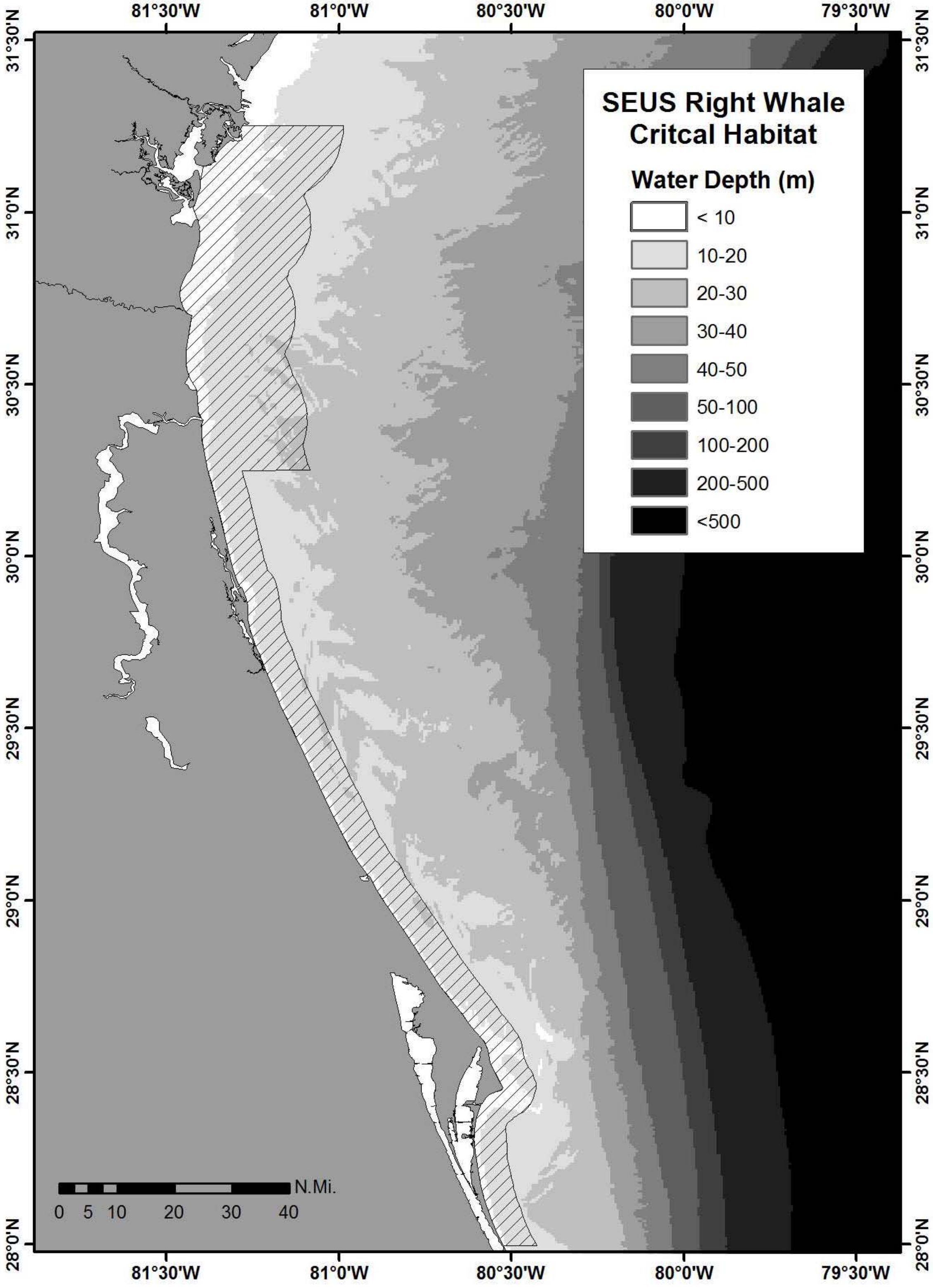


Figure 2. Raster grid representation of aerial survey effort (number of flights) between the 1992/1993 – 2000/2001 right whale calving seasons. The currently designated calving critical habitat is shown (cross-hatch).

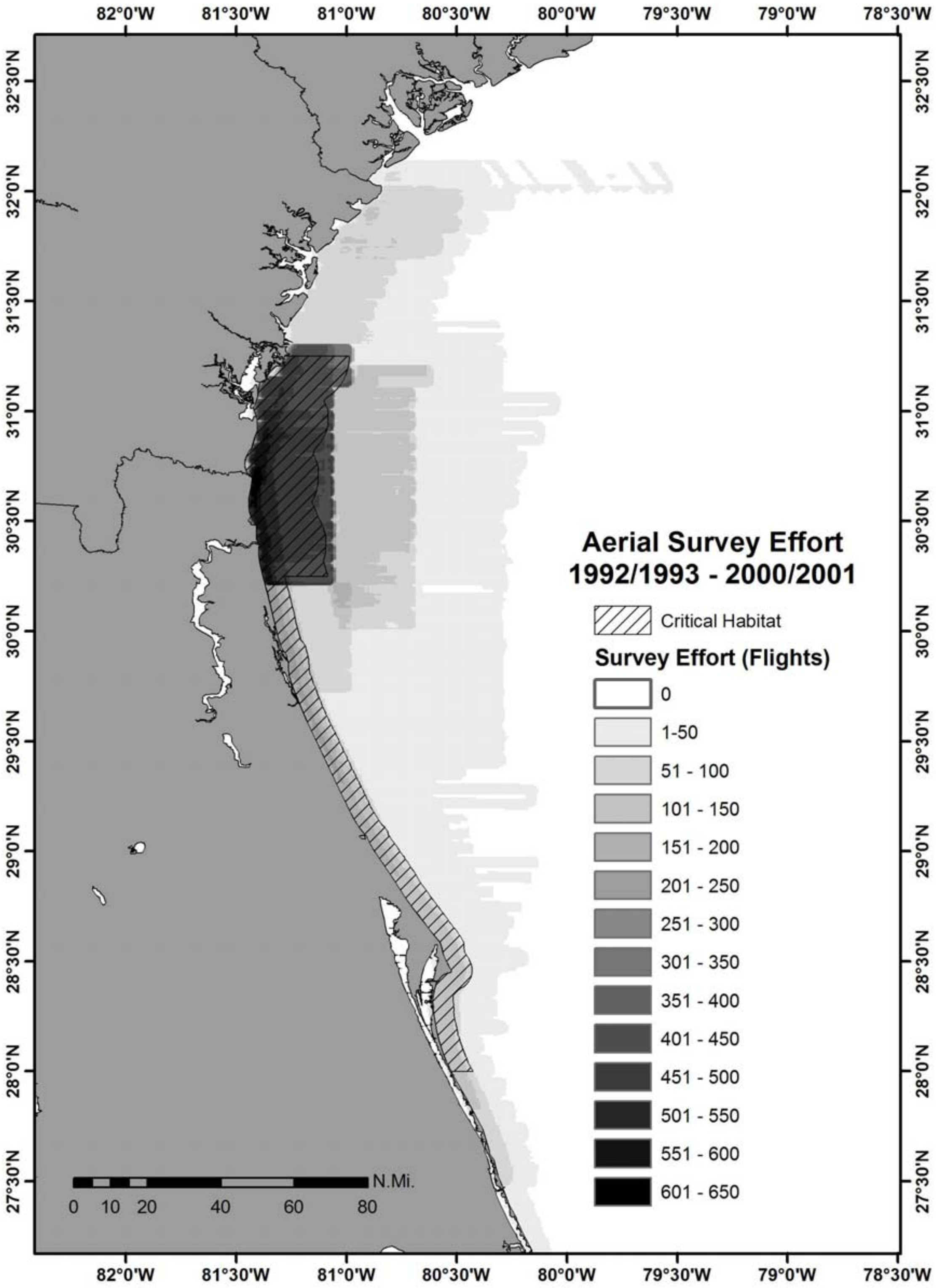


Figure 3. Location of calving female right whale sightings during standardized survey effort between the 1992/1993 – 2000/2001 right whale calving seasons. The currently designated calving critical habitat is shown (cross-hatch).

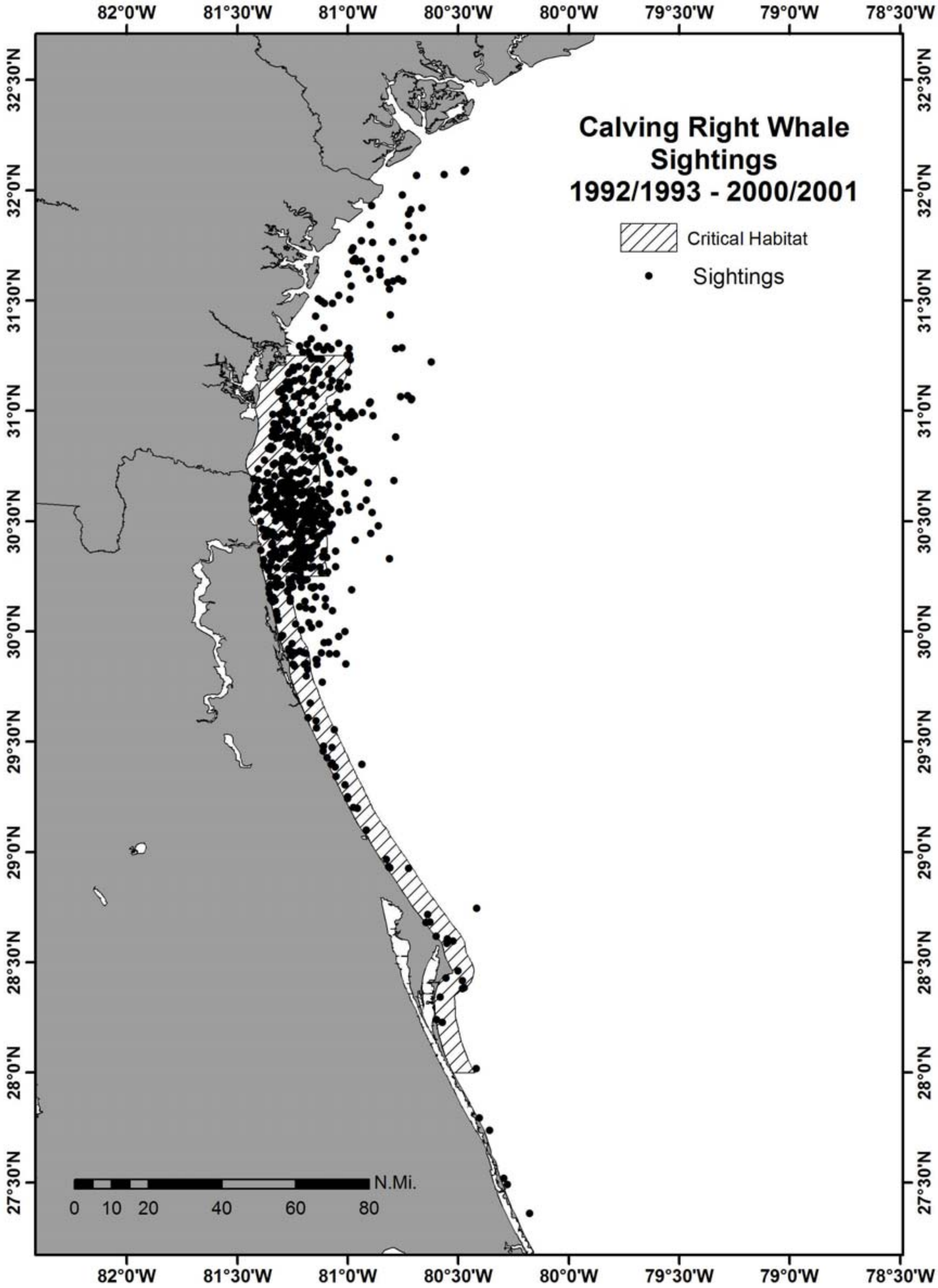
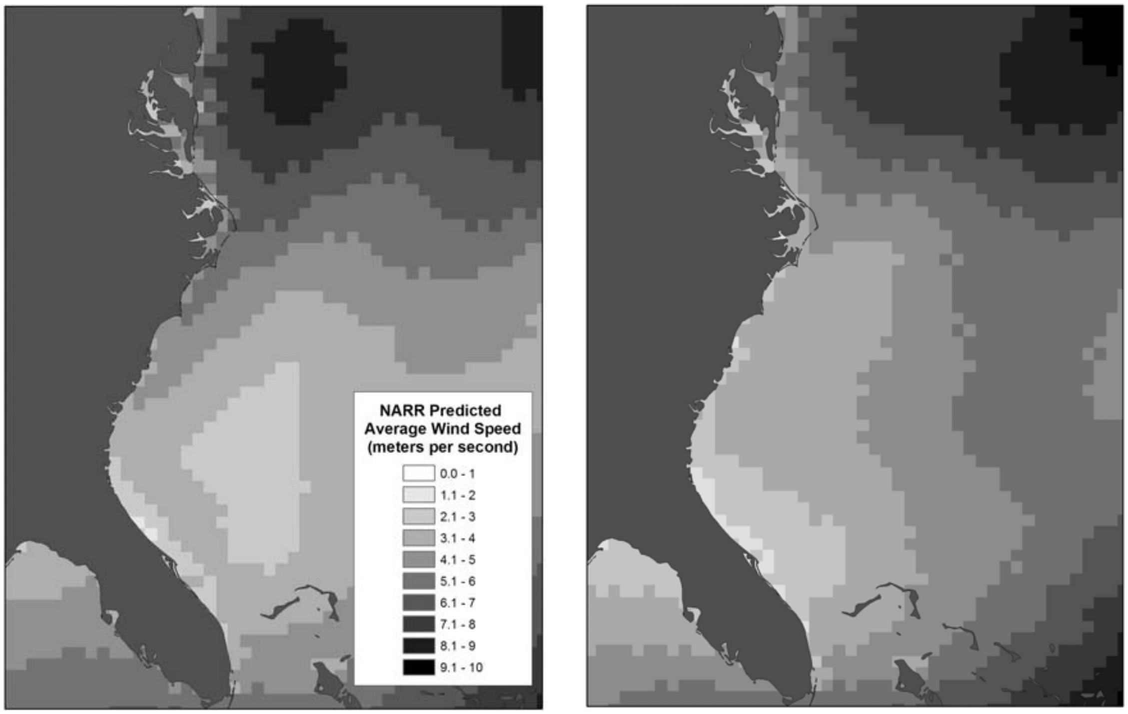
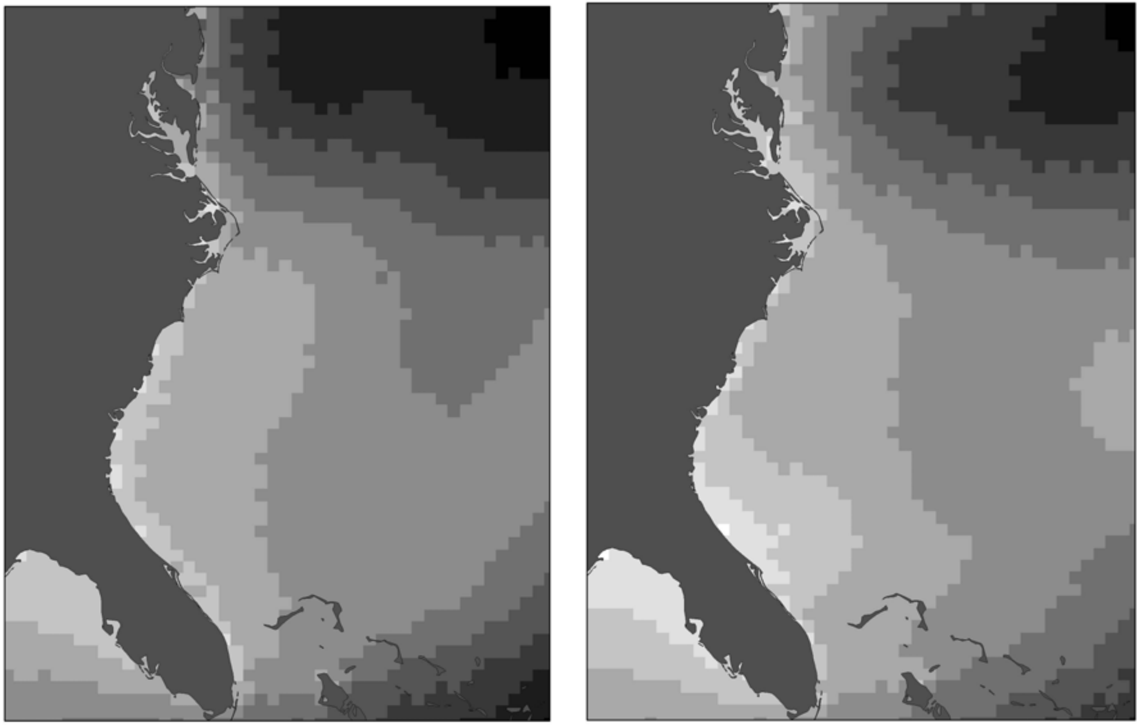


Figure 4. Regional monthly average wind speeds at 10m above ground as predicted by the NARR climate model. Wind speeds (m/s) are averaged for each month across the 1992/1993 – 2000/2001 survey seasons. Annual monthly average wind speeds were used in the construction of the habitat model.



A. December

B. January



C. February

D. March

Figure 5. Spatial cells (4x4 km) used to aggregate environmental and sightings data in the GAM analysis. Total calving right whale sightings within each spatial cells across the entire time series is shown.

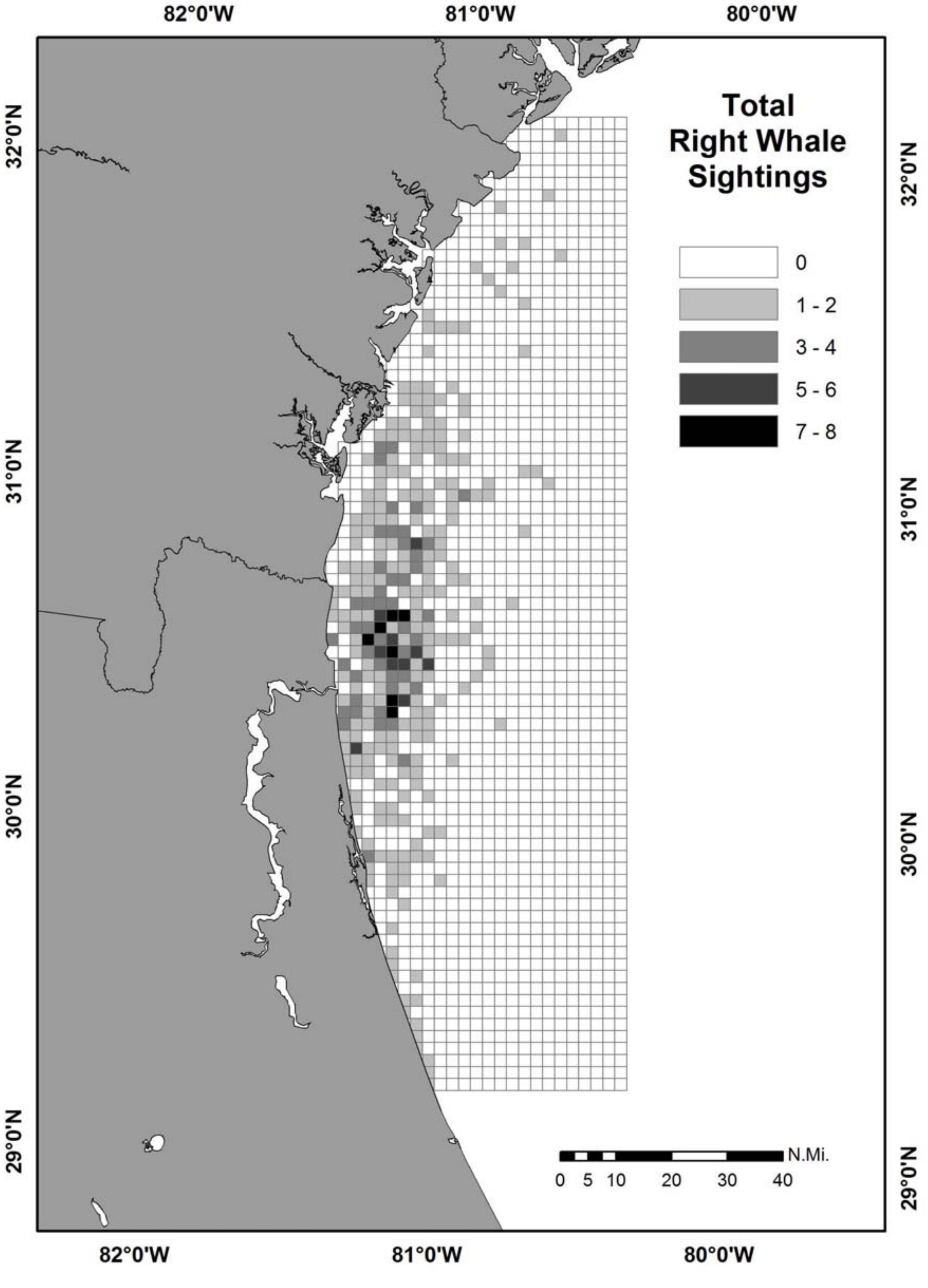


Figure 6. Observed and predicted total right whale sightings for each survey season. Error bars indicate the 95% Confidence Interval of the bootstrap distribution.

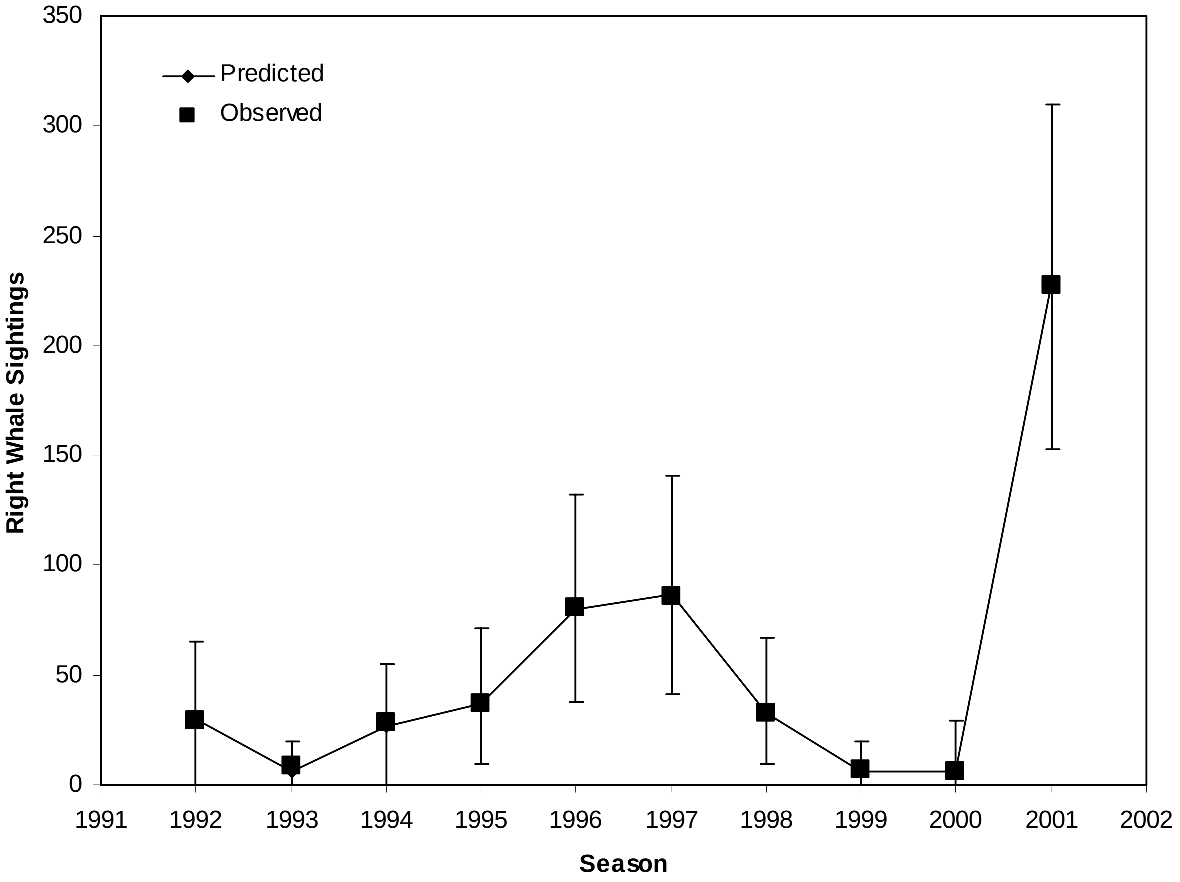


Figure 7. Observed and predicted sightings by depth (1 meter) and temperature (1 degree C) cells averaged across survey years. Error bars indicate 95% confidence bounds from the bootstrap distribution of predicted values. Note differences in y-axis scales.

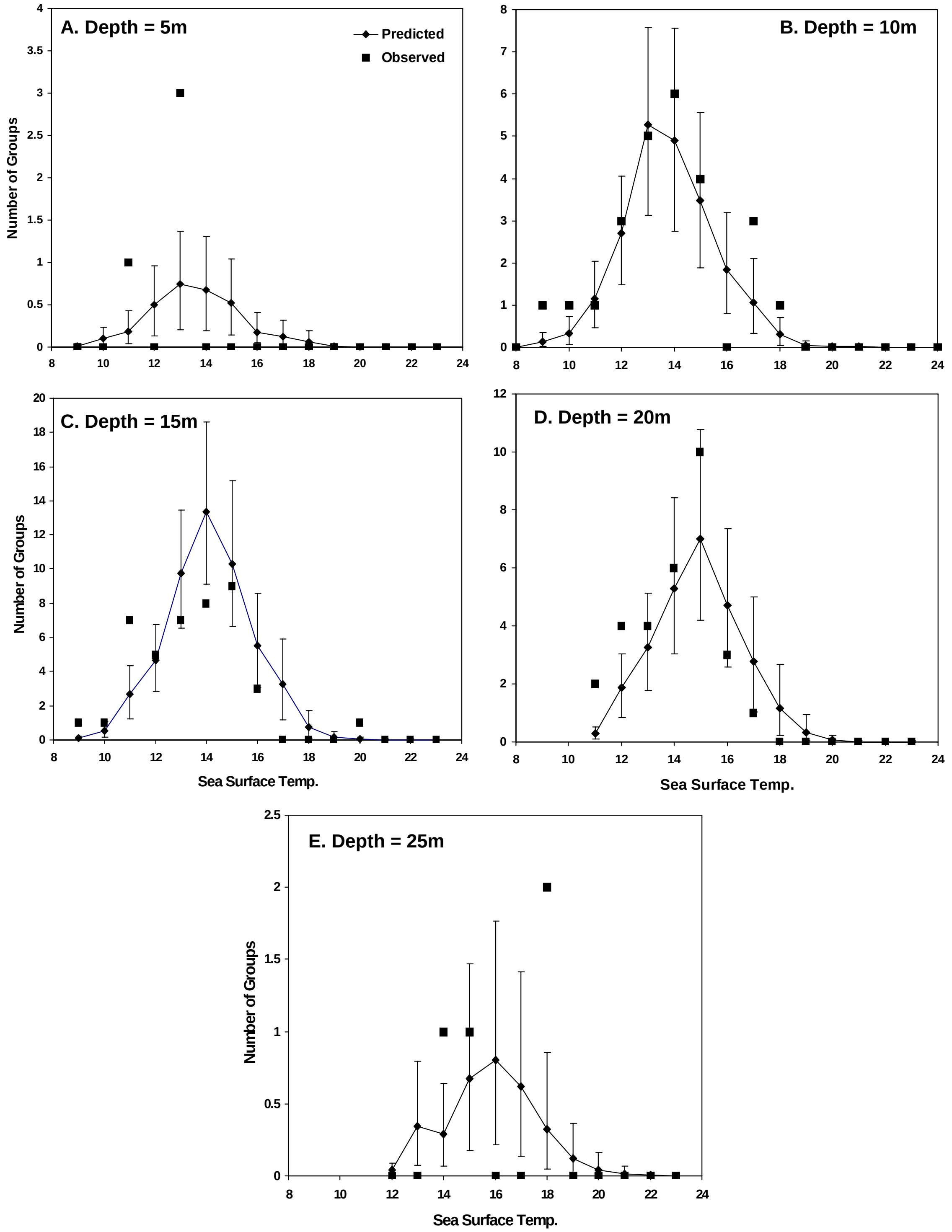


Figure 8. Surface plot of median predicted sighting rates (Sightings per Unit Effort) from bootstrap distribution by water depth and temperature intervals.

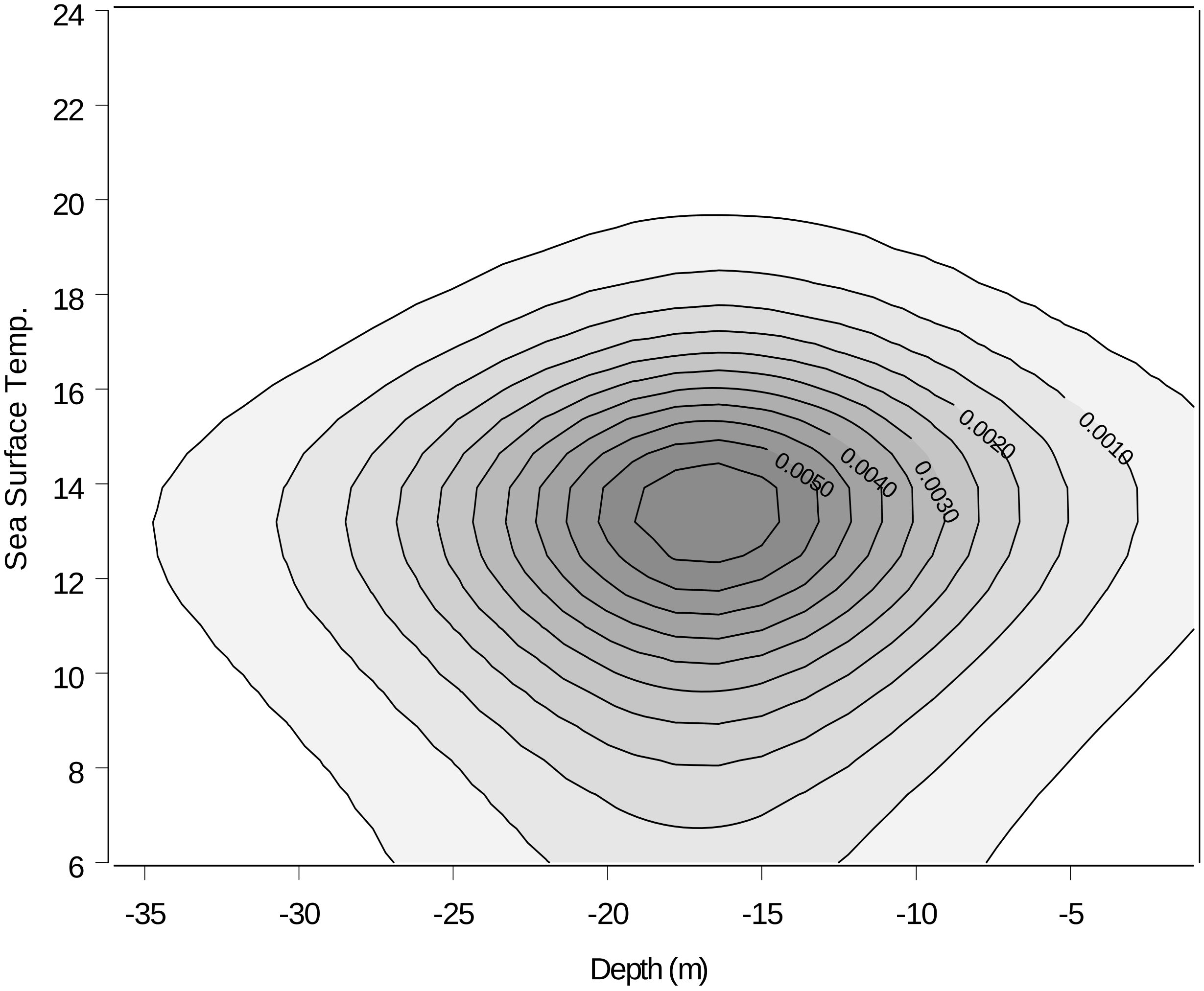


Figure 9. Correlation between observed and predicted right whale groups in 1-m depth and 1°C temperature intervals during the (A) 1996/1997 and (B) 2000/2001 survey seasons.

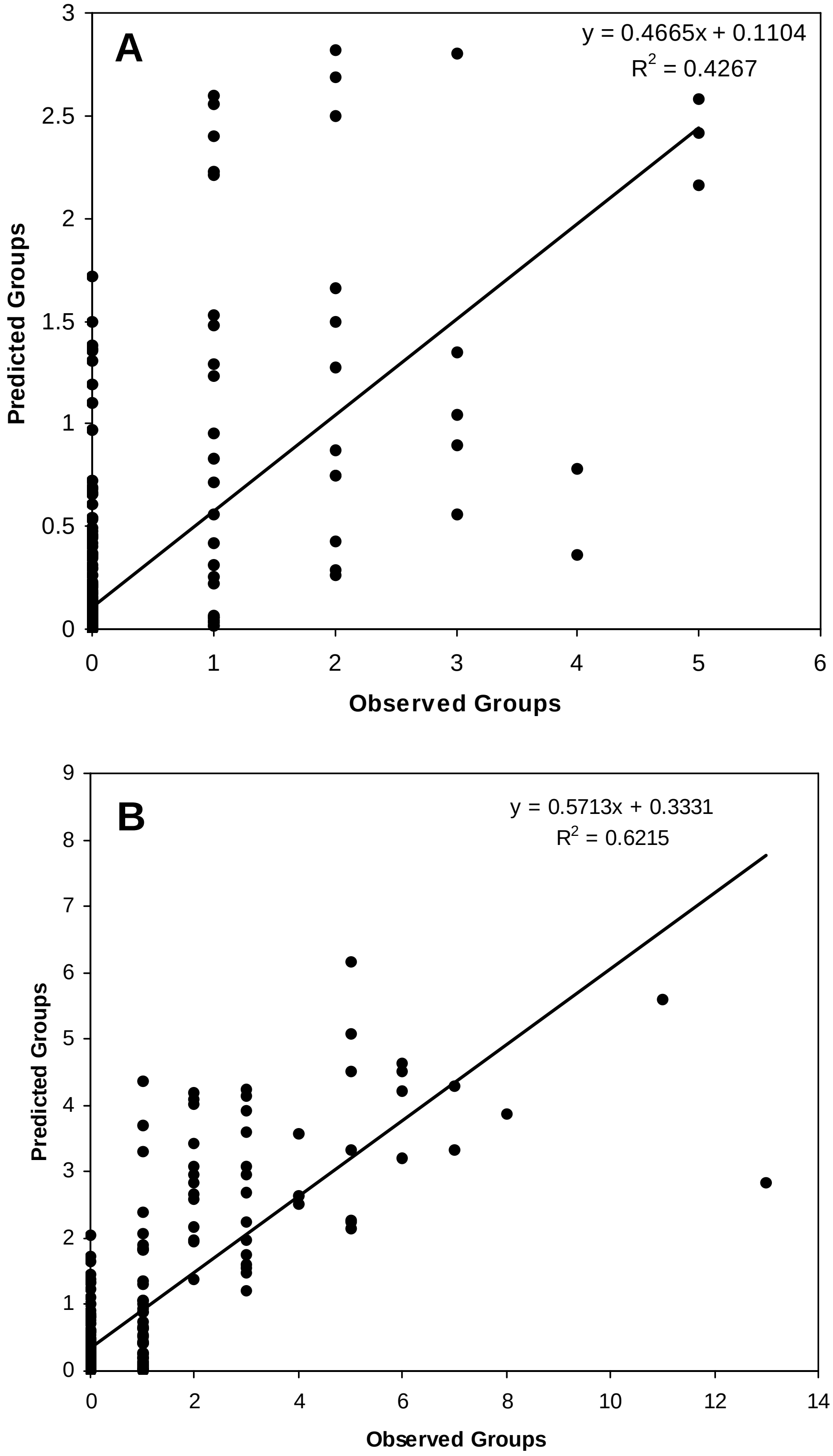


Figure 10. Predicted sighting probability and observed sighting locations for right whales during the 1996/1997 survey year.

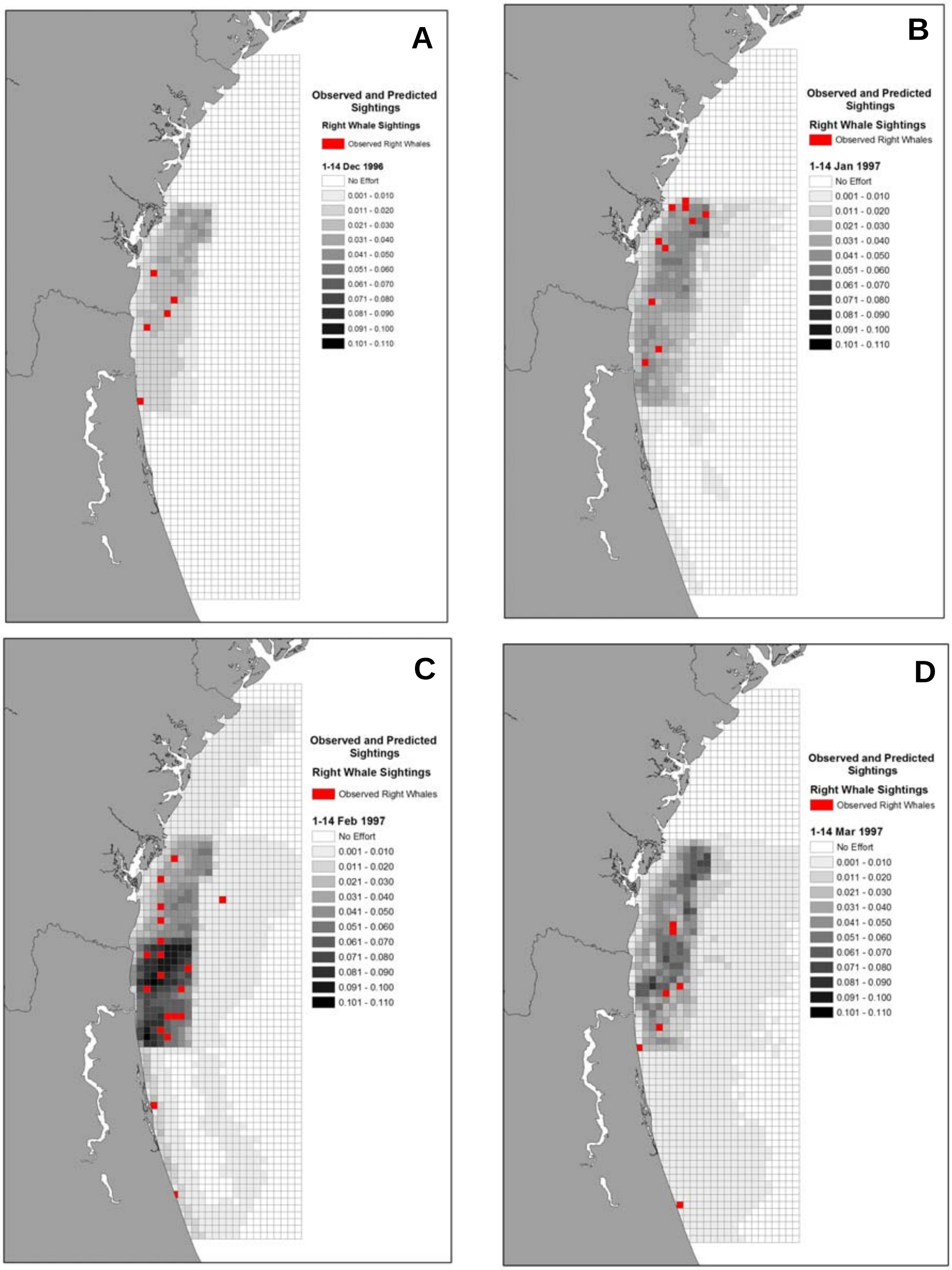


Figure 11. Predicted sighting probability and observed sighting locations for right whales during the 2000/2001 survey year.

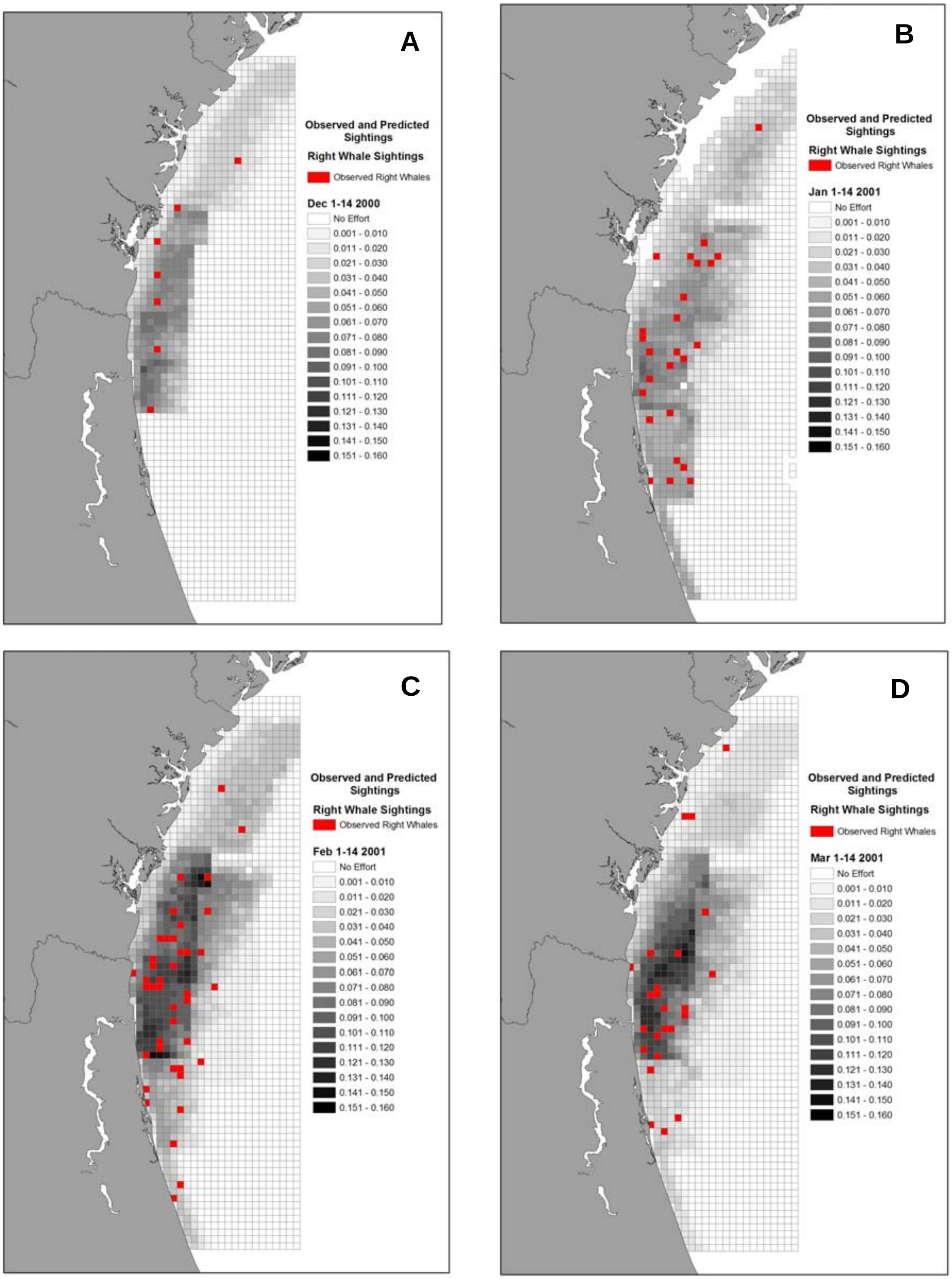


Figure 12. Average predicted SPUE and sea surface temperature across the survey time series for the month of December.

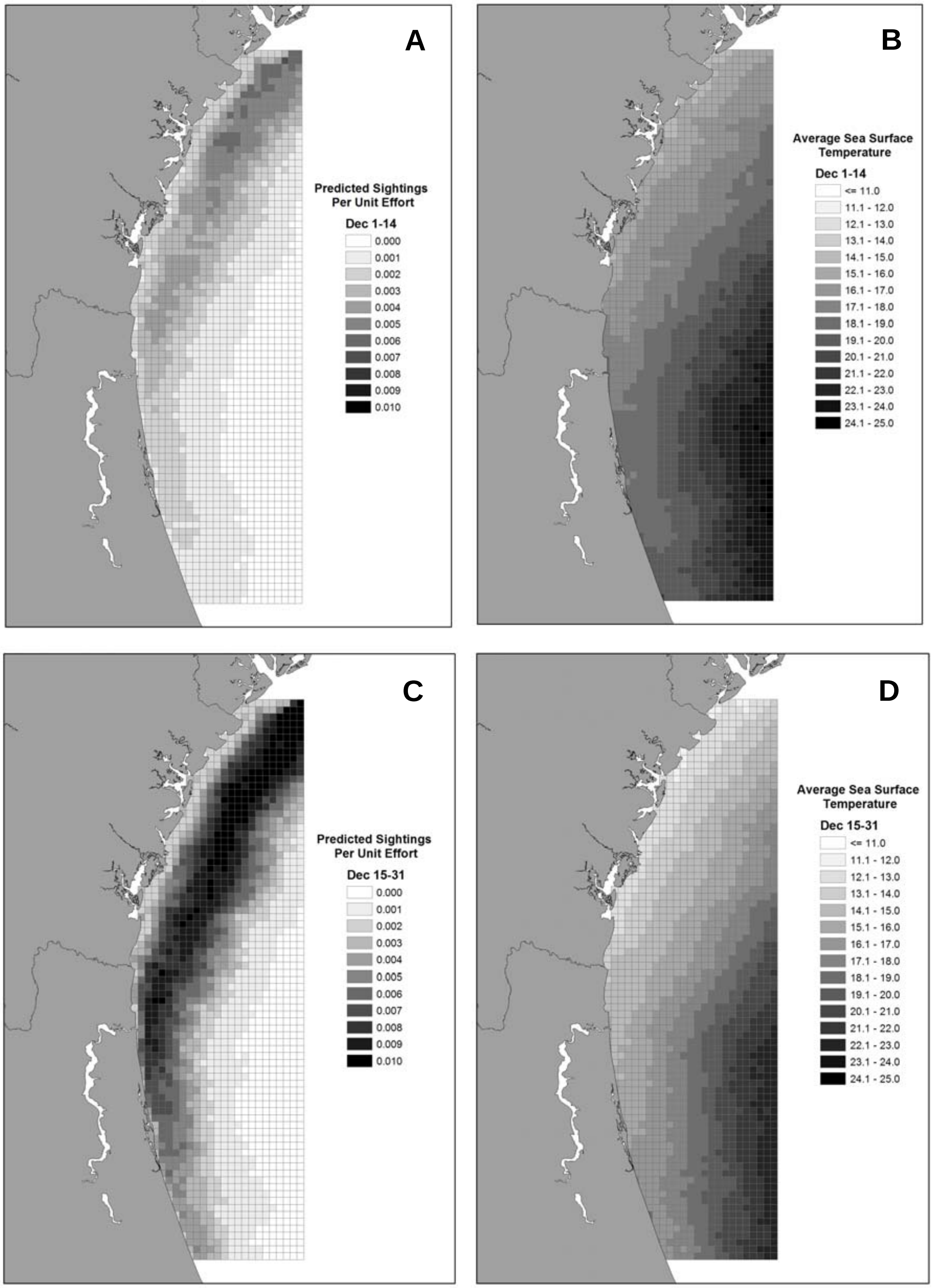


Figure 13. Average predicted SPUE and sea surface temperature across the survey time series for the month of January.

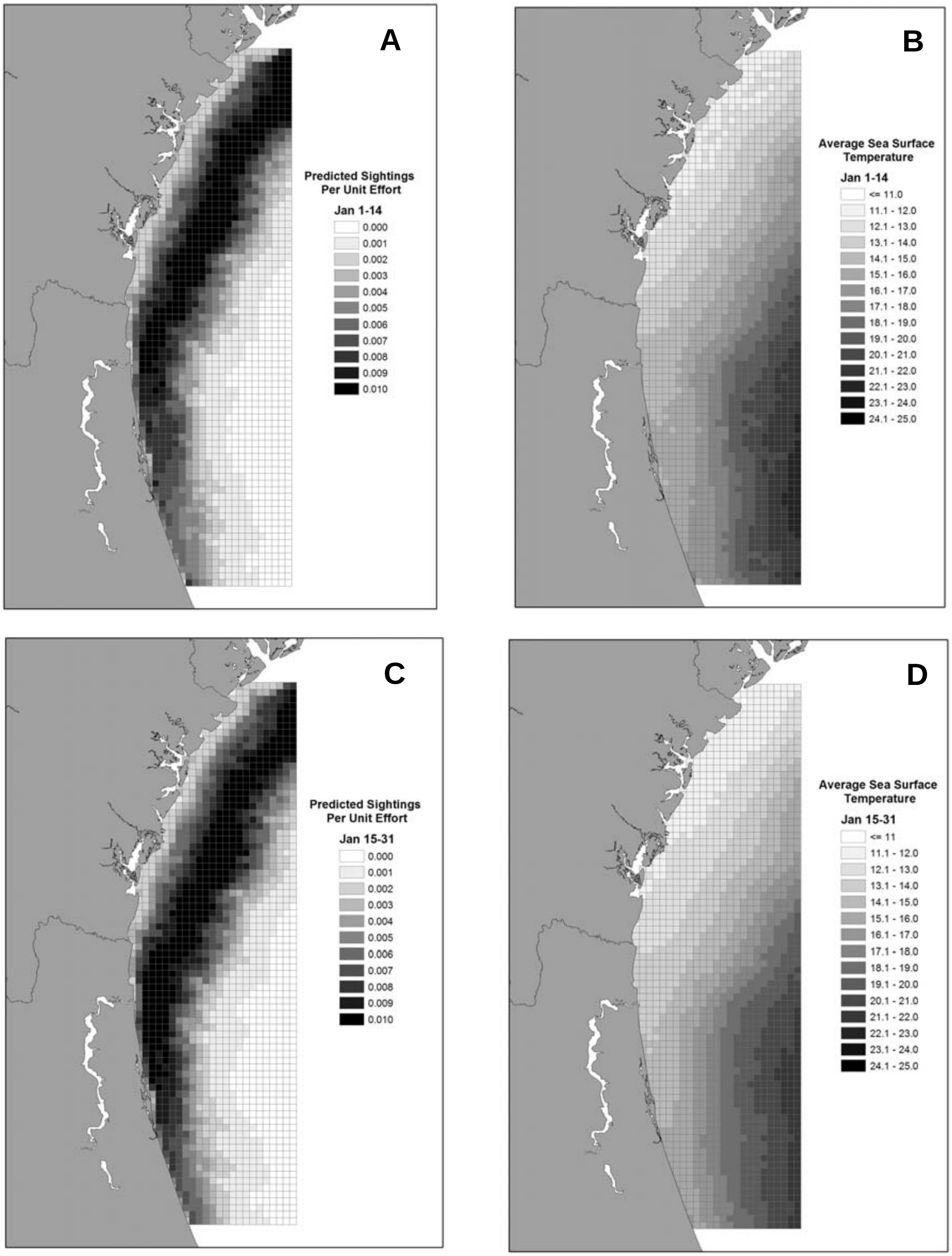


Figure 14. Average predicted SPUE and sea surface temperature across the survey time series for the month of February.

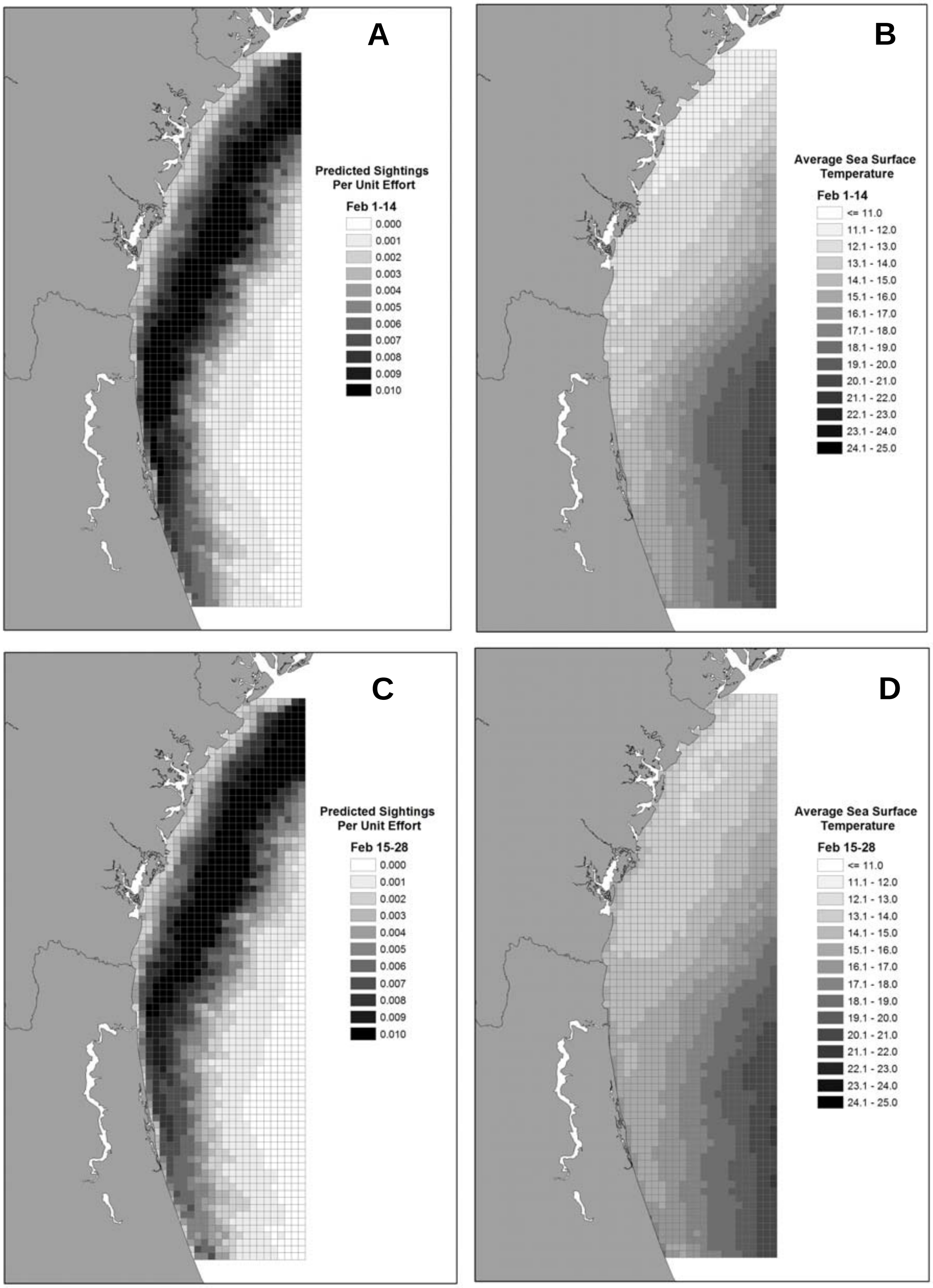


Figure 15. Average predicted SPUE and sea surface temperature across the survey time series for the month of March.

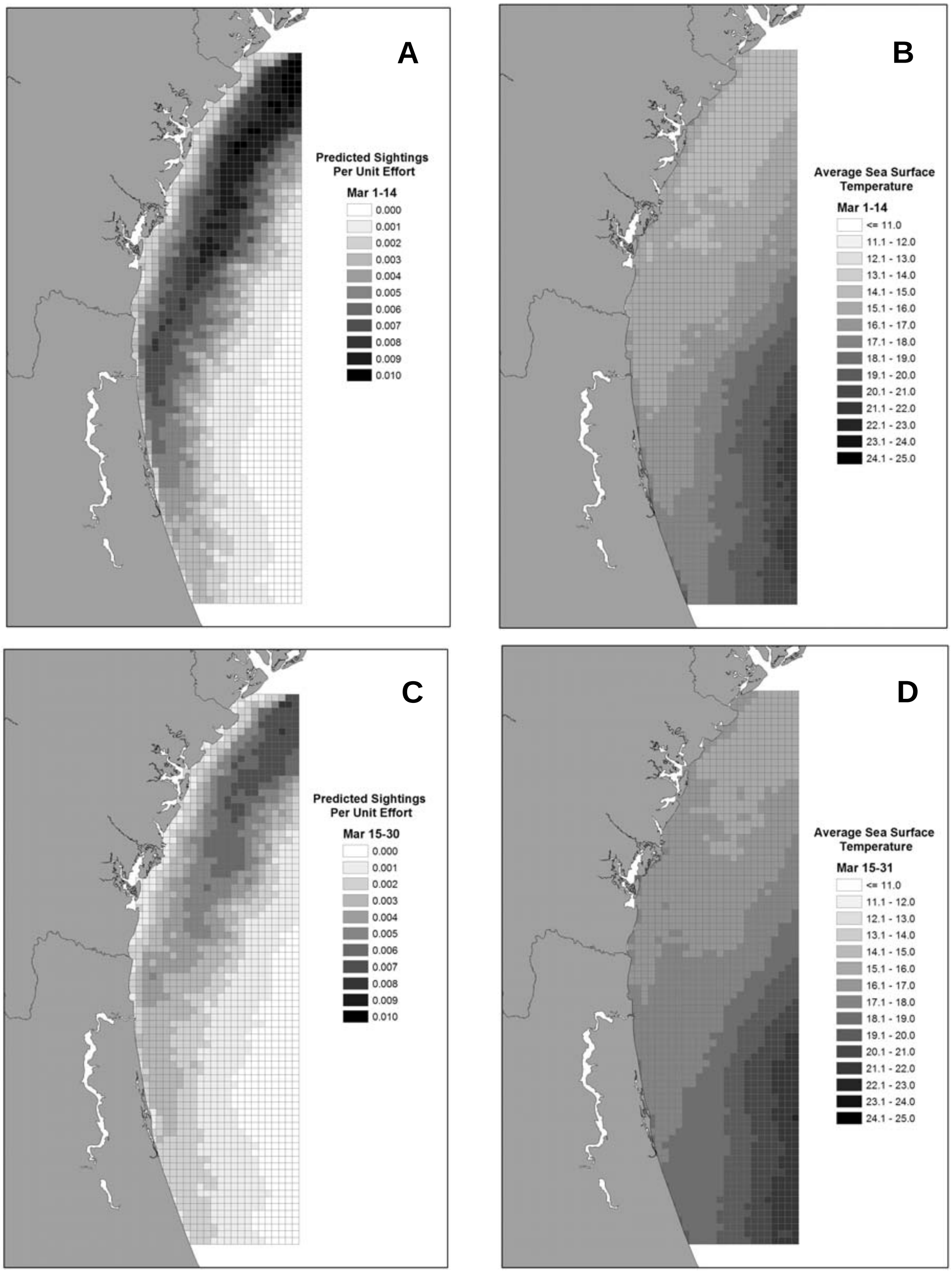


Figure 16. Percentile of predicted sightings per unit effort by water depth and temperature intervals.

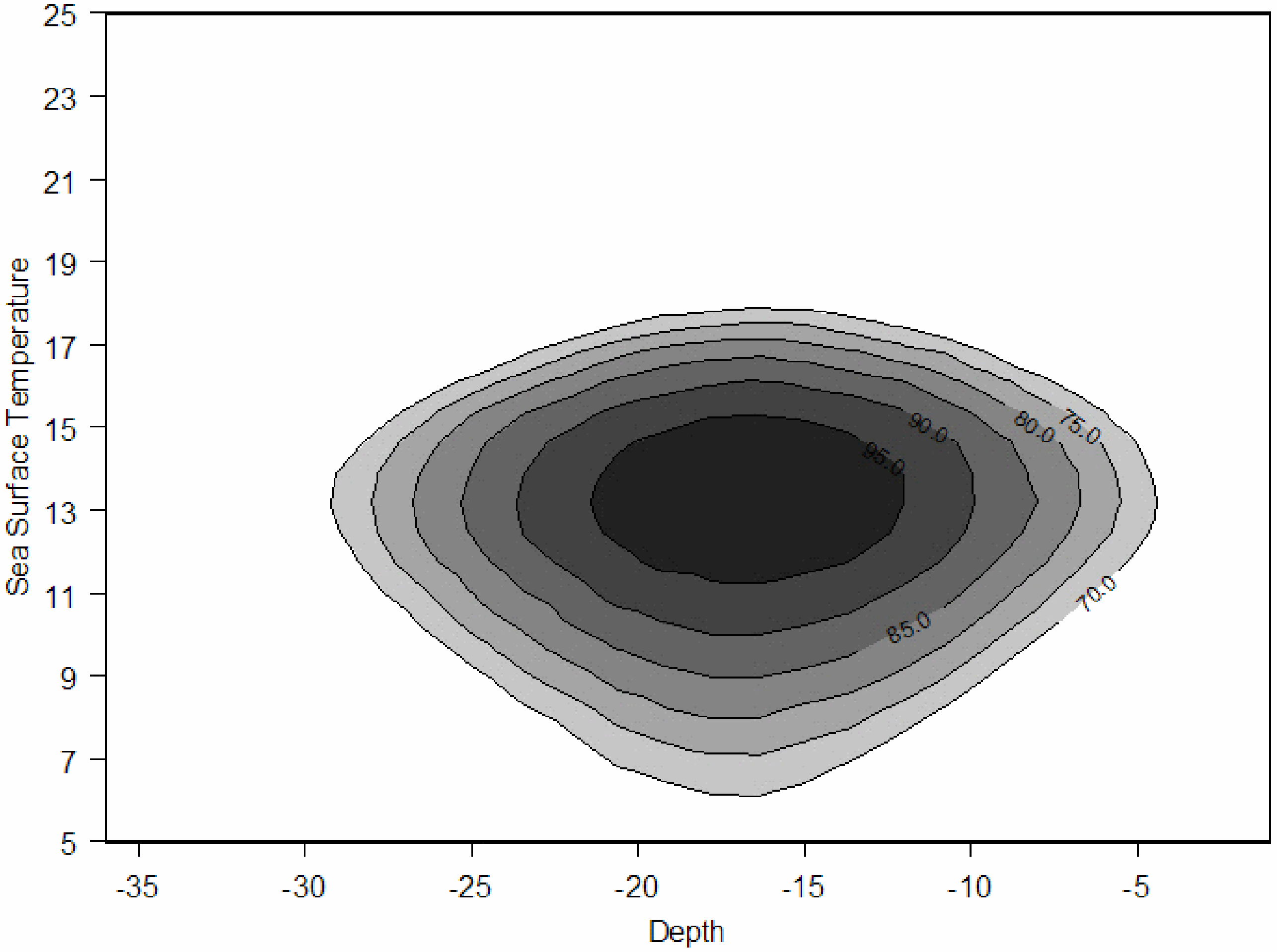


Figure 17. Cumulative proportion of observed right whale groups and survey effort by percentile of predicted sightings per unit effort.

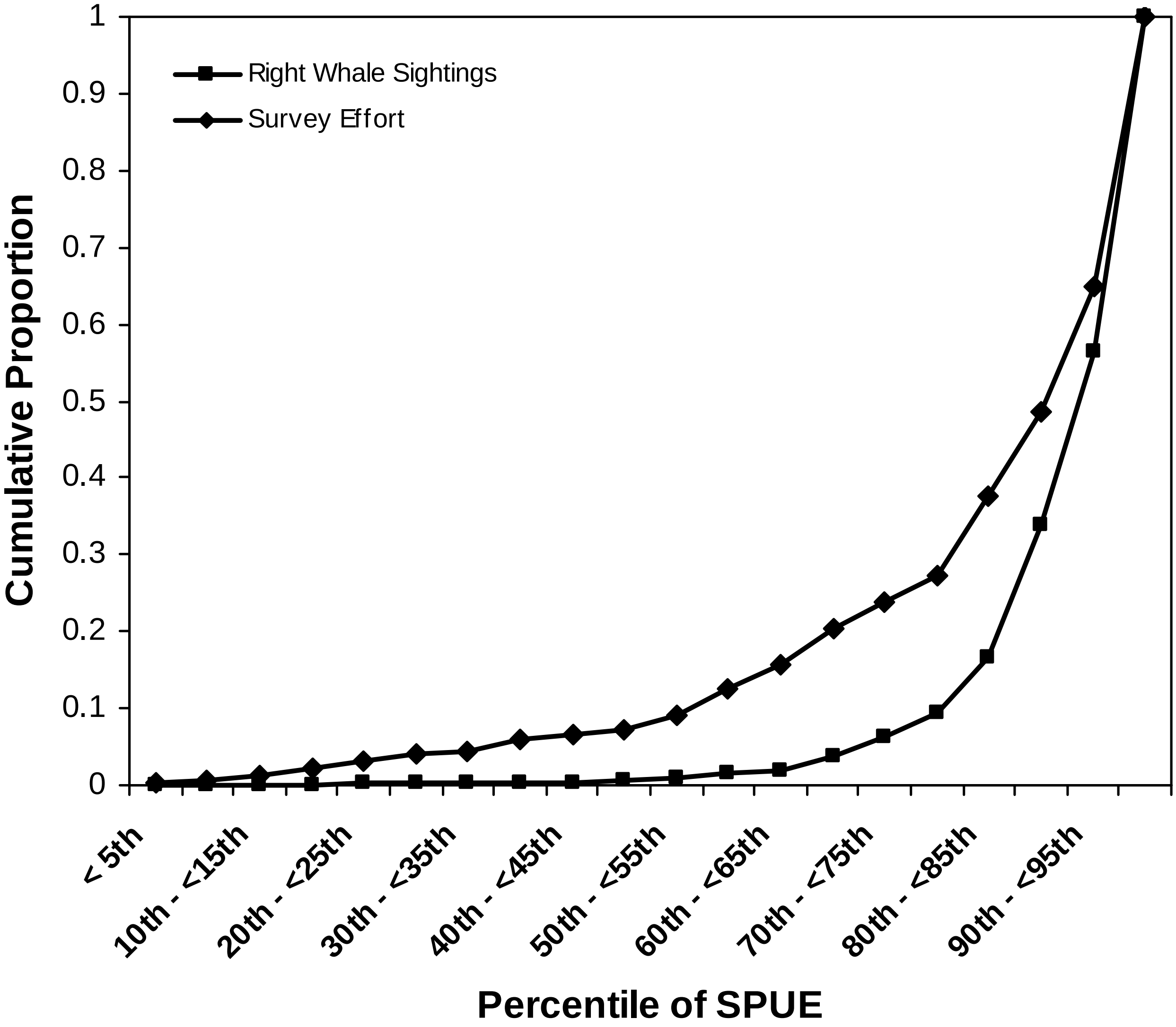


Figure 18. Average sea surface temperature (A) and resulting predicted percentile of sightings per unit effort (B).

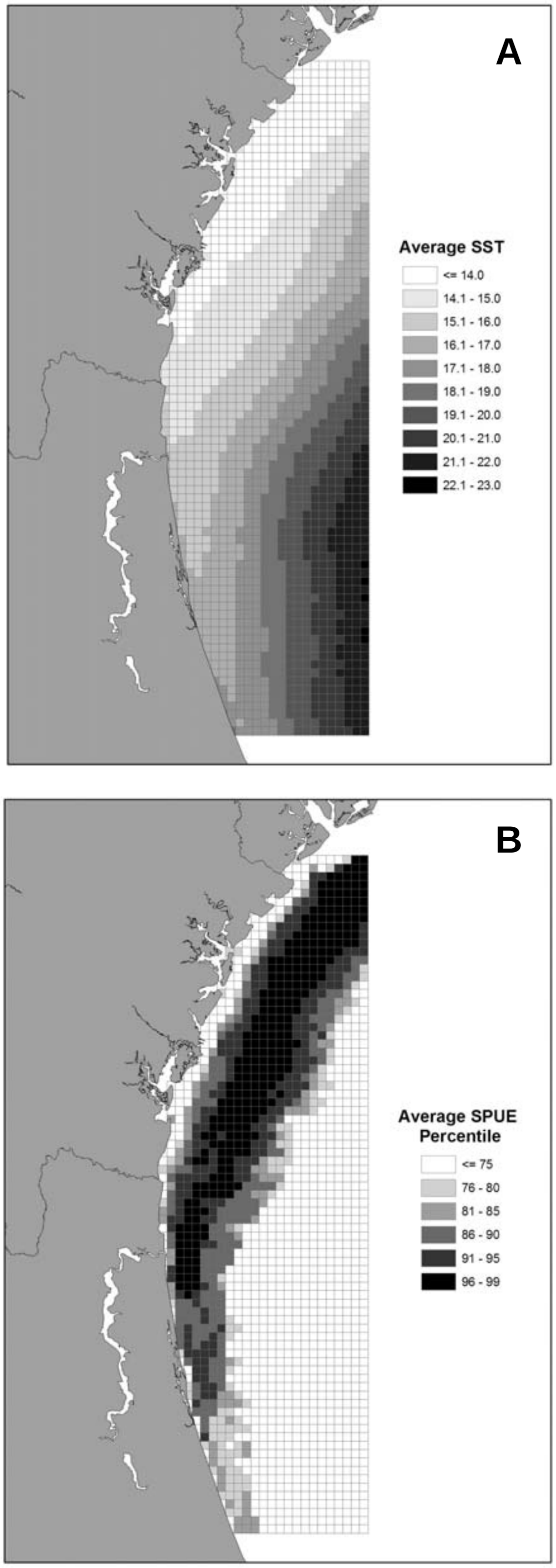


Figure 19. Potential static critical habitat boundaries based upon percentiles of predicted SPUE. The currently defined calving habitat boundary is shown as a dotted line.

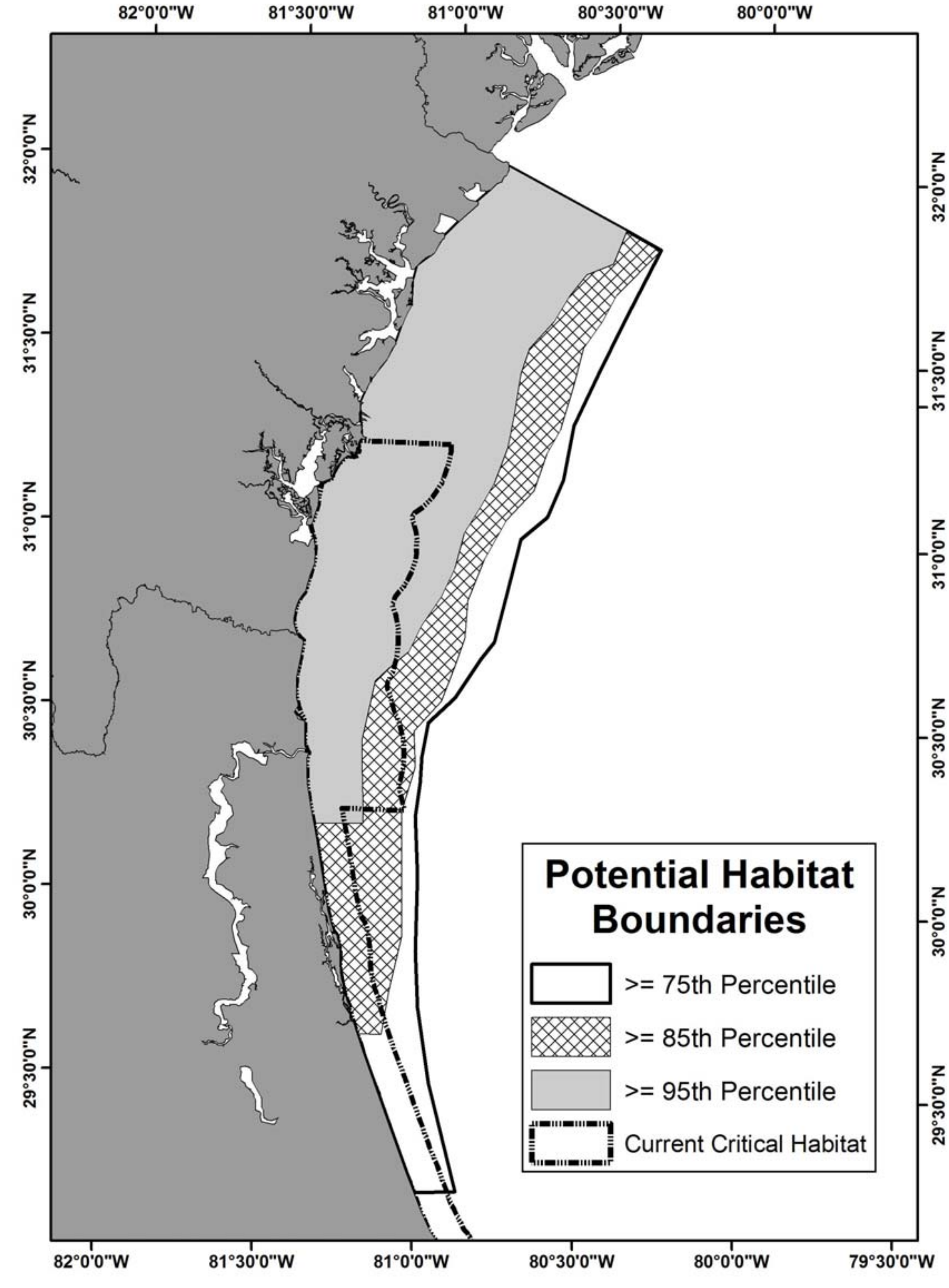


Figure 20. Regional bathymetry along the southeastern U.S. Atlantic coast.

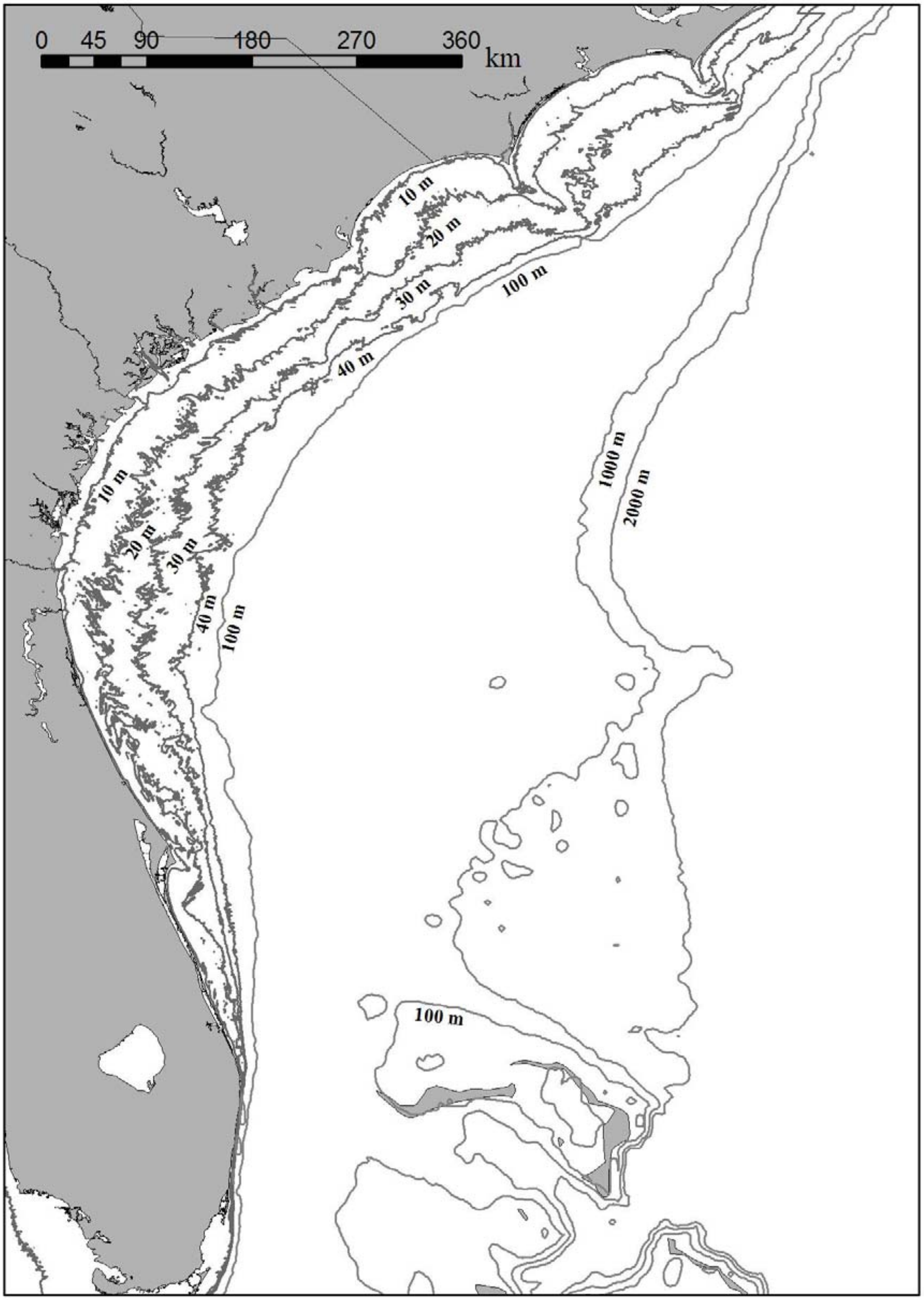


Figure 21. Monthly Average Sea Surface Temperature along the U.S. Mid-Atlantic coast derived from satellite imagery.

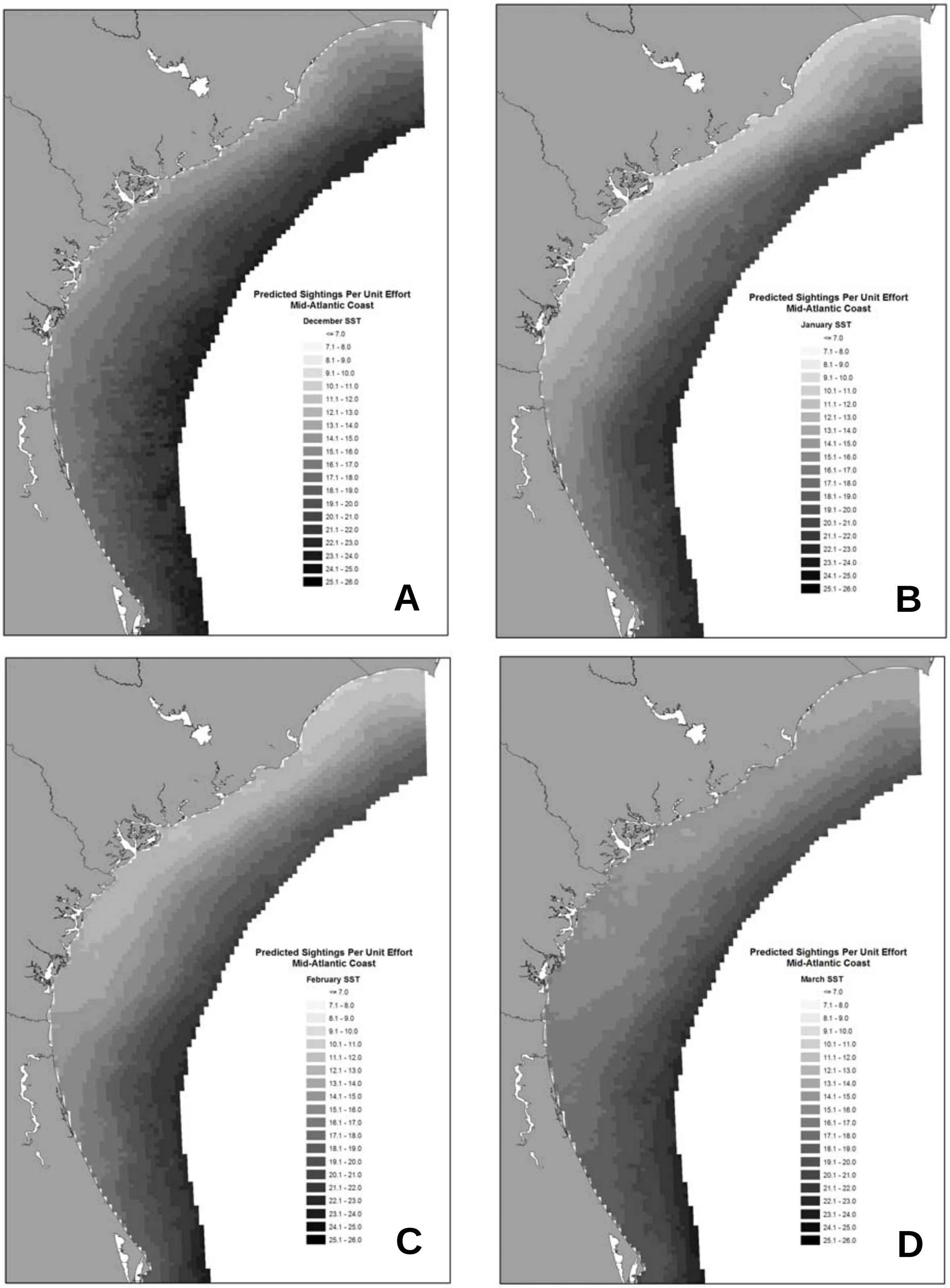


Figure 22. Predicted sightings per unit effort along the U.S. mid-Atlantic coast based upon monthly average sea surface temperatures.

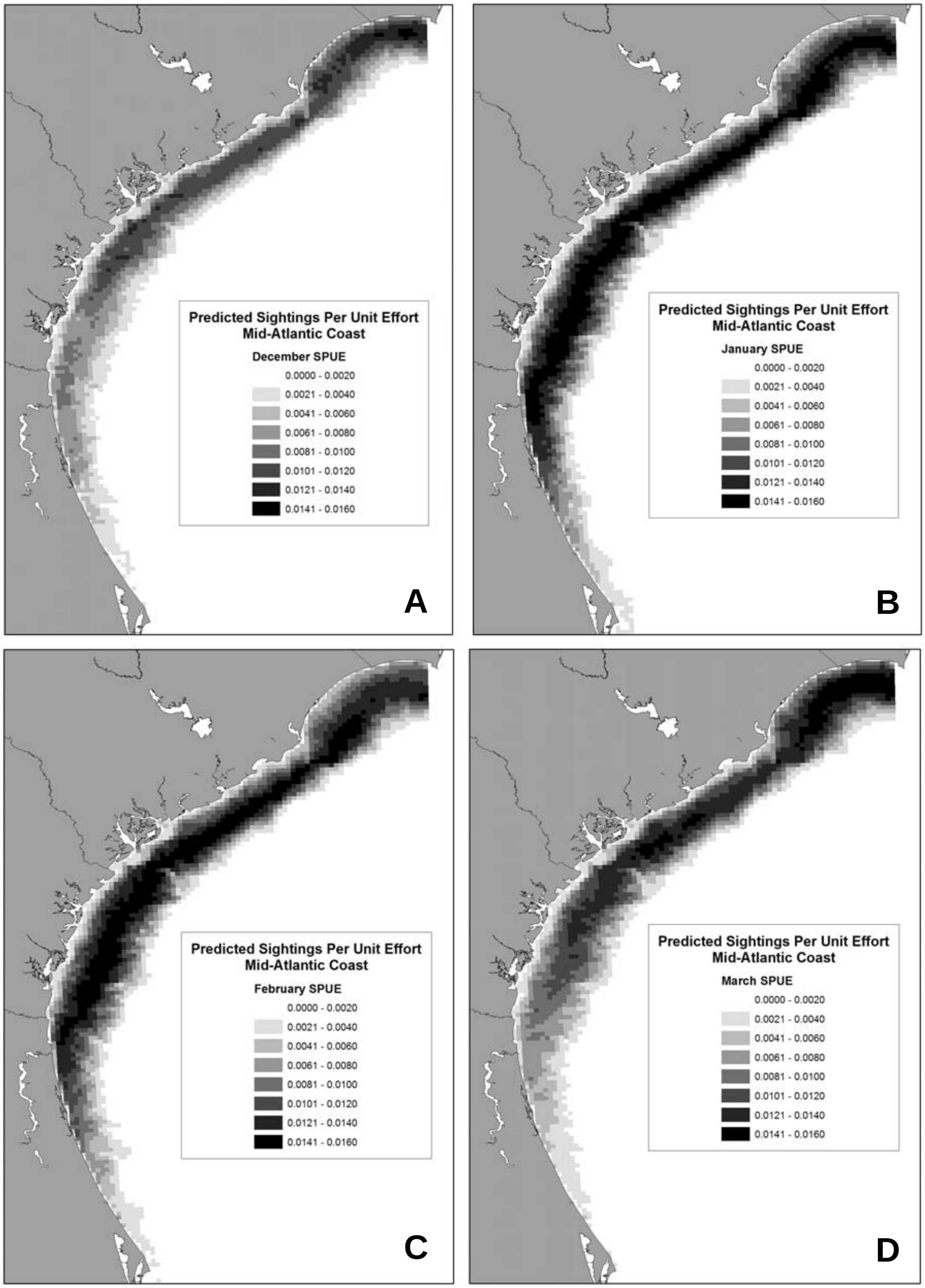


Figure 23. Sightings per unit effort percentiles along the mid-Atlantic coast based upon average sea surface temperatures during December – March.